THE BIOLOGY OF SOME NEW ZEALAND BLEPHAROCERIDAE (DIPTERA:NEMATOCERA).

A thesis presented for the degree of Doctor of Philosophy in Zoology.

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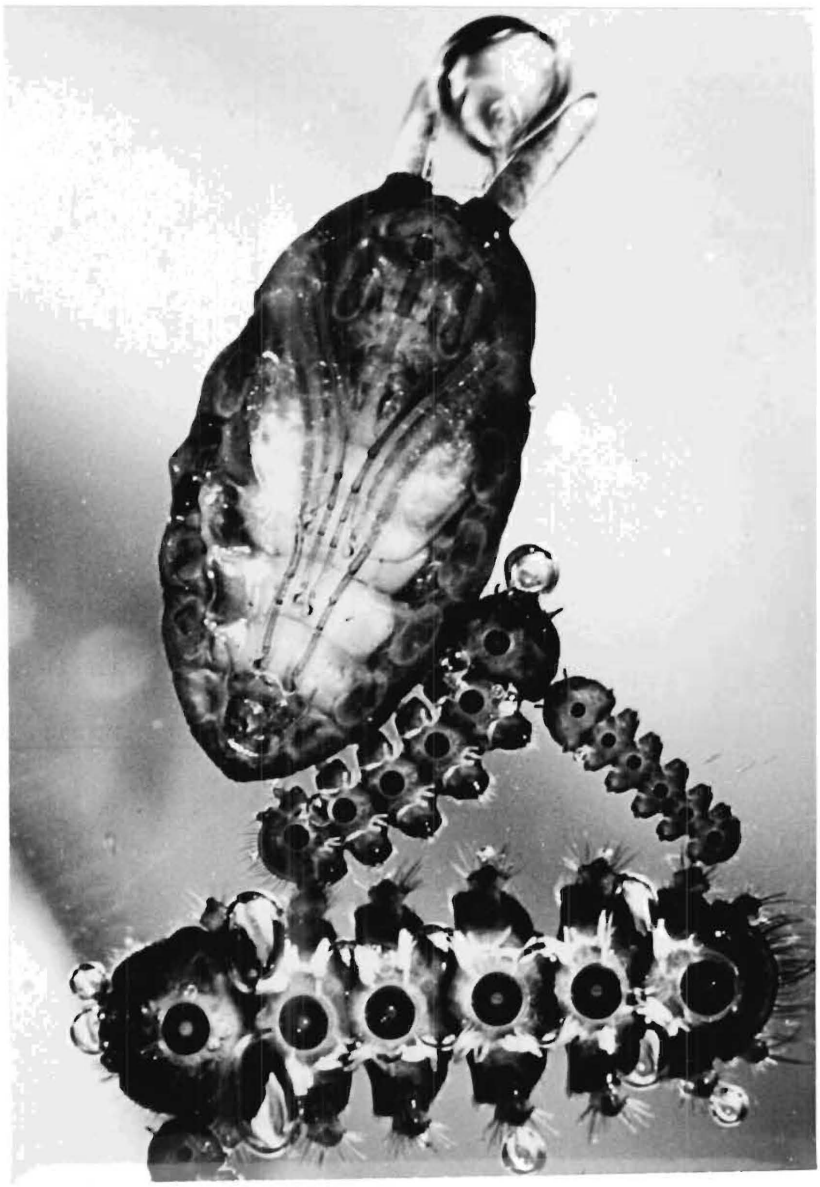
CHRISTCHURCH.

1966

FRONTISPIECE

Second, third and fourth instar larvae, and pupa of *Neocurupira chiltoni*.



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PREFACE

When this study was commenced during late 1962, little was known concerning the biology of New Zealand blepharocerids and the most recent work with any bearing on them was by Tonnoir (1930). Dumbleton (1963) described new species and extended the areas of distribution of the known species, but discussed few biological aspects.

As so little was known concerning the biology of New Zealand blepharocerids, a more general study was necessary rather than an investigation of a few aspects more closely. However, it is hoped that some of the more interesting aspects of this initial work will be further investigated.

The thesis has been presented as a series of separate chapters with their own pagination, for it was originally intended, if time permitted, to publish some of the chapters as separate papers. This was not completely possible, but to this end Chapter II and some of the Appendixes are already in press.

This thesis has been printed by the Multilith process with consequent loss of fine detail in some figures, especially those of Chapter II.

Dumbleton, L.J., 1963: New Zealand Blepharoceridae (Diptera: Nematocera). N.Z.J.Sci., 6, 2: 234-258.

Tonnoir, A.L., 1930: Notes on Indian Blepharocerid Larvae and Pupae with remarks on the Morphology of Blepharocerid Larvae and Pupae in General. Rec.Indian.Mus., 32, 2: 161-214.

ACKNOWLEDGMENTS

I would like to thank the following:-

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My supervisors, Dr V.M. Stout, Professor R.L.C. Pilgrim and Dr E.C. Young for their guidance, encouragement and constructive critisism during the study for and the writing of this thesis.

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R.E.G. Craig, for drawing the graphs in Chapter III and helping with the proof-reading of this thesis.

Those, too numerous to name, who helped in many ways, particularly in the collection of blepharocerid material.

ABSTRACT.

Chapter I.

New blepharocerid material, related to Neocurupira is described as Forms A, B, C and D, and placed along with N. hudsoni in a hudsoni- complex. On the basis of variation in eye structure within the hudsoni- complex the subgenus Paracurupira is shown to be unwarranted.

Because of the morphological similarities of the eggs, larvae and adults, N. chiltoni and N. tonnoiri are considered to constitute a species group. On the basis of larval and adult morphology, Peritheates intermedius is considered to be synonymous with P. turrifer.

The areas of distribution of known New Zealand blepharocerids are given.

Descriptions and keys to most of the larval instars of known New Zealand blepharocerids are given, as well as keys to the adults of Australasian genera of blepharocerids.

The origin and evolution of Australasian and in particular New Zealand blepharocerids are considered. It is believed that blepharocerids arrived in New Zealand from the north,along land bridges, during the late Cretaceous. There is no evidence to suggest that Australian blepharocerids gave rise to New Zealand blepharocerids.

Chapter II.

The eggs of Neocurupira campbelli, N. chiltoni, N. hudsoni and N. tonnoiri are figured and described. The embryonic development of N. chiltoni is traced and, less fully, that of N. campbelli. Comparisons are made between the embryology of N. chiltoni and N. campbelli and that of certain chironomids, culicids and simuliids.

It is concluded that the similarities existing between the embryology of the simuliids and blepharocerids may indicate phylogenetic affinities.

Chapter III.

The study areas, Purau Stream, Kaituna River and Bealey River, as well as some other blepharocerid habitats, are described and their similarities listed.

The records of rainfall, temperatures and water levels from the study areas are given and some of their interrelationships considered. The effects of floods on the study areas and larval populations are considered.

The velocity, oxygen saturation, dissolved solids and pH of the water in the study areas are considered and the relationships between water velocity, larval respiration rate and sucker attachment are discussed.

It is concluded that the operation of the sucker is the main factor which enables blepharocerid larvae to inhabit swiftly flowing water.

The more important floral and faunal associates are listed and the effects of the density and types of associates on larval blepharocerids are considered.

The distribution of larvae in the study areas is considered and some of the possible limiting factors discussed. Water velocity is believed to be the main limiting factor.

Movement of N. chiltoni larvae is described and the observations compared with previous work on other blepharocerid species.

The movement and function of the larval mouth parts are described and figured. Observations show that larvae prefer thin layers of algae but do not select particular algal types.

Prepupae select suitable pupation sites. The prepupae of N. campbelli and P. turrifer in contrast to those of N. chiltoni, form dense aggregations. The pupation sites of N. hudsoni are unknown. Pupae in swiftly-flowing water orientate the anterior end downstream.

The attachment of the N. chiltoni larvae during pupation is considered. Observations indicate that the larval suckers maintain their attachment to the substrate until the cement secreted by the pupa hardens and the larval cuticle is sloughed off.

The emergence of N. chiltoni adults is described and the part played by the hydrophobic nature of the adult body during emergence, ovipositioning and the avoidance reaction is considered.

Normal flight, as well as the avoidance reaction, is described.

The mouth parts and the anterior part of the alimentary canals of N. chiltoni and N. hudsoni are compared with those of Liponeura cinerascens a known predaceous blepharocerid. It is postulated that New Zealand blepharocerids do not feed, but may be able to take up water.

The mating and oviposition behaviour of the adult blepharocerids studied is described and the difference exhibited by N. chiltoni established. In contrast to other New Zealand blepharocerids N. chiltoni oviposits below the surface of the water.

Laboratory data and field observations on the longevity of N. chiltoni adults are given. The laboratory data shows that there is no significant sexual difference , but the field observations indicate that the males live longer than do the females. The effects of a sexual difference in life span is considered and it is believed that this contributes to the imbalance of the sexes in adult collections.

The sampling techniques used to determine life cycles are described and it is shown that at Purau and Kaituna N.chiltoni probably has two generations per year, whereas at Bealey Chasm N. campbelli, N. hudsoni and P. turrifer have only one generation a year, though some of the larvae take longer than one year to complete development. The differing life cycles are considered

to be the result of temperature difference between the two localities.

The sex ratio of pharate N. campbelli adults is shown to vary seasonally and to have a significant negative regression on mean water temperature, whereas that of N. chiltoni remains relatively constant throughout the year.

The percentage of brachypterous pharate N. campbelli females is also shown to have a seasonal change and a significant negative regression on mean water temperature. It is suggested that the variations in sex ratio and in brachypterism are interrelated.

CHAPTER I.

A TAXONOMIC REVISION OF NEW ZEALAND BLEPHAROCERIDAE AND THE ORIGIN AND EVOLUTION OF THE AUSTRALASIAN BLEPHAROCERIDAE.

INTRODUCTION

Chilton (1906) reported the discovery in 1900 by G.R.Marriner of blepharocerid larvae at Lake Coleridge, Canterbury, and his own discovery (in 1903) of blepharocerid larvae at Akaroa, Banks Peninsula. Because the Banks Peninsula larvae showed similarities to the South American genus Curupira, Chilton designated them as "? Curupira". From material collected at Arthur's Pass by G.V.Hudson, Lamb (1912) erected two new genera, Neocurupira and Peritheates, designating N. hudsoni and P.turrifer, respectively, type species. Bezzi (1914) provided description of three forms of larva collected by Chilton at Akaroa.

Campbell (1921) made a detailed study of the Banks Peninsula blepharocerid which he named Curupira chiltoni. He also attempted to identify the three forms of larva supplied to Bezzi by Chilton, but produced a considerable amount of confusion in the process. Later (Campbell, 1923), he showed that the three forms of larva described by Bezzi were only larval instars of Curupira chiltoni. Campbell (1921) described and named new blepharocerid adults and larvae from Ohakune, North Island as Apistomyia harrisi and reported the occurrence of blepharocerids at Dunedin and Queenstown.

Tillyard (1922a), in a revision of the N.Z. Blepharoceridae, described a new species, Peritheates intermedius, and transferred Apistomyia harrisi Campbell to Peritheates. He also transferred Curupira chiltoni to a new genus Paracurupira on the basis of the dichoptic males of C. chiltoni and the holoptic males of Neocurupira

hudsoni. Edwards (1929), in discussing the general classification of Blepharoceridae, relegated Paracurupira to subgeneric rank. Kitakami (1950), Alexander (1958) and Dumbleton (1963a) also consider Paracurupira to be subgeneric.

Tonnoir (1923b; 1930b) discussed the rearing of blepharocerid larvae, described the pupation of Peritheates intermedius Tillyard and mentioned a new form of Neocurupira larva but did not provide a description. Dumbleton (1963a) described two new species, Neocurupira (Paracurupira) tonnoiri (which was the form mentioned by Tonnoir 1923b) and N. (P) campbelli. As well as erecting a new subgenus Austrocurupira for the Australian species N.nicholsoni Tillyard, he presented keys to the known adults and 4th instar larvae of New Zealand blepharocerids and discussed the affinities and biology of New Zealand species of blepharocerid.

In this paper, new dichoptic male adults, closely related to N. hudsoni are described, and the species Peritheates intermedius and the subgenus Paracurupira are shown to be invalid.

Descriptions are given of larval instars, most of which have not previously been described, and keys to adults and larvae are provided. Although full descriptions of previously described species are not given, their important characters are utilized in the keys.

A description of first instar larvae of N. chiltoni is provided, though it is as yet not possible to identify species by first instar larvae.

The possible origin and evolution of New Zealand and Australian Blepharoceridae are discussed.

METHODS

Descriptions are based on specimens preserved in Andres Fluid or, more rarely, in 70% alcohol. The storage of all stages of blepharocerid material in fluid is recommended as it prevents the shrinkage of taxonomically important genitalia and head structures that is often met with on pinned specimens.

All drawings were made, using a squared eye piece, on "Ethulon" plastic over graph paper.

Colour descriptions of larvae and adults are based on The Geological Society of America "Rock Color Chart", 1951, which is itself based on Munsells colour system.

Locality Records.

Locations cited are arranged in approximate order of North to South and East to West. Map references following locations refer to Department of Lands and Survey 1" to 1 mile Topographical Maps, (N.Z.M.S.I.).

Abbreviations.

The letters L., P. and A. indicate positive identification of either larvae, pupae, and adults in the sample. A query e.g. L? indicates a doubtful identification.

The following abbreviations are used to indicate collectors:-

D.A.C. - D.A.Craig.

L.J.D. - L.J.Dumbleton.

V.M.S. - V.M.Stout.

Institutions housing material are indicated:-

Auck. Mus. - Auckland Museum.

Dom. Mus. - Dominion Museum.

Cant. Mus. - Canterbury Museum.

Ent. Div. N. - Entomology Division, Department of Scientific and Industrial Research, Nelson.

Ent. Div. L. - Entomology Division, D.S.I.R., Lincoln.

Uni. Auck. - University of Auckland, Zoology Department.

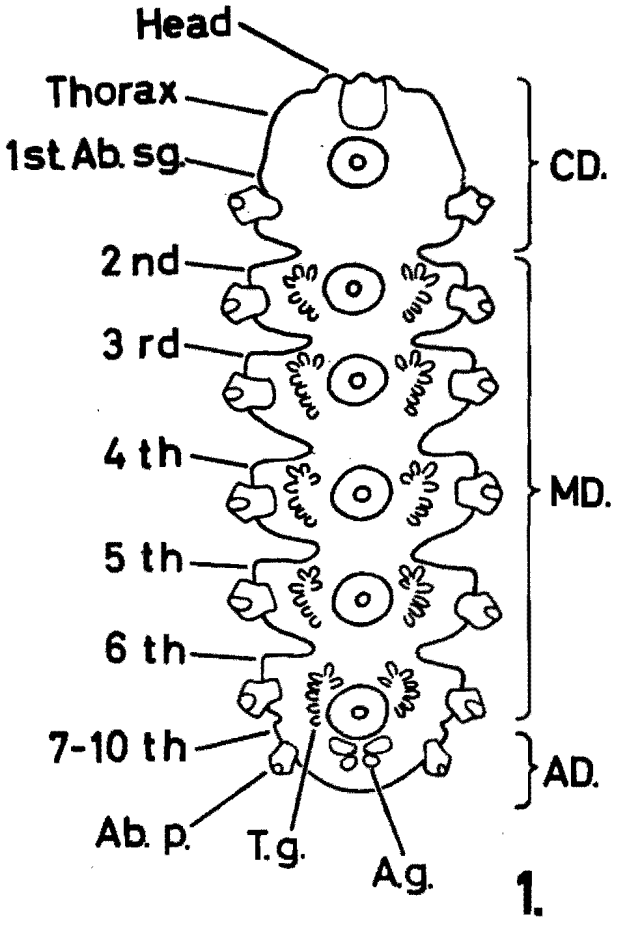
(Misc) following locations indicates that the sample is housed in the Miscellaneous Freshwater Collection, Zoology Department, University of Canterbury.

Numbers in parentheses, e.g. (23), following locations indicate the number of the sample in the Freshwater Collection, Zoology Department, University of Canterbury. Numbers underlined, e.g. 23, indicate samples housed in the private collection of Dr.V.M.Stout, Zoology Department, University of Canterbury.

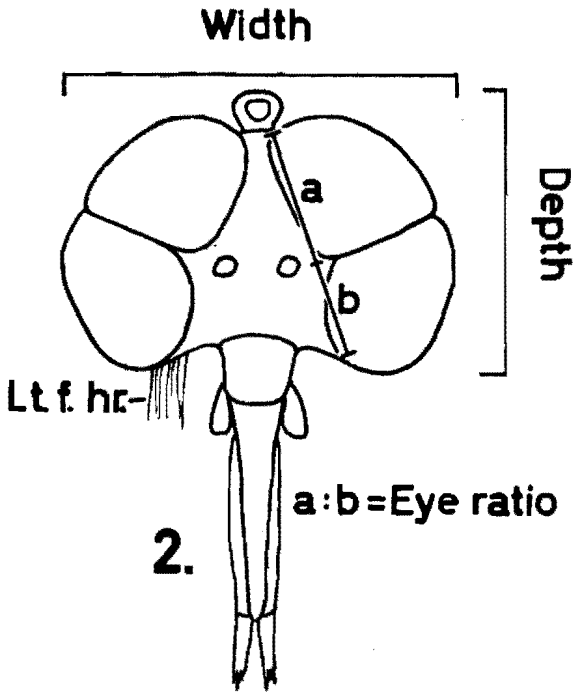
TERMINOLOGY

Adult:

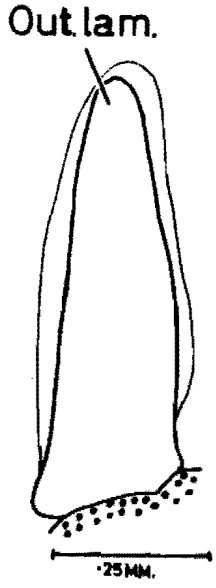
Head: Previously the relationship between the estimated areas of the upper and lower eyes was used as an diagnostic character. As this


Head
Thorax
1st Ab. sg.
2 nd
3 rd
4 th
5 th
6 th
7-10 th
Ab. p.
T.g.
A.g.
CD.
MD.
AD.

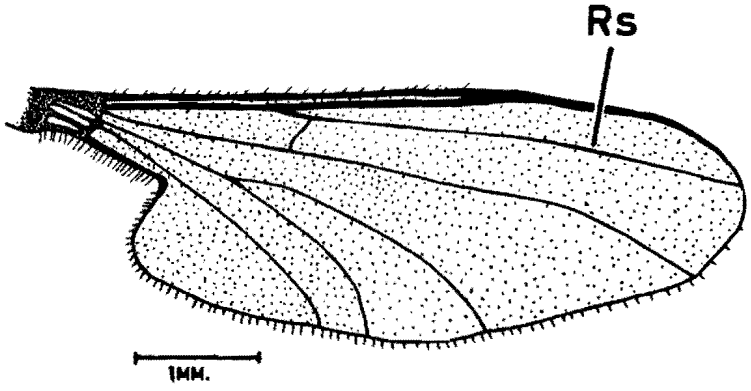
1.


Width
Depth
a
b
Lt f. hr.
a : b = Eye ratio

2.


Out. lam.
·25 MM.

3.


Rs
1MM.

4.

Chapter I.

Figures:-

1. Diagram of fourth instar blepharocerid larva showing the relationship of divisions to body segments.
2. Diagram of frontal view of male adult blepharocerid head, illustrating ratios used in descriptions.
3. Anterior lamellae of Form D pupal gill.
4. Wing of P.turrifer male.

Abreviations:-

1st. Ab. sg.	- First Abdominal segment.
2nd - 10th	- Second to tenth Abdominal segments.
A. g.	- Anal gills.
Ab. p.	- Abdominal proleg.
AD.	- Anal Division.
CD.	- Cephalic Division.
Lt. f. hr.	- Lateral facial hairs.
MD.	- Median Divisions.
Out. lam.	- Outer lamella.
T.g.	- Tracheal gills.

ratio is not sufficiently accurate to demonstrate variation in the eye structure of new material described here, a more accurate ratio describing the relationship of the upper eye to the lower eye has been devised. This ratio called the eye ratio is calculated using measurements taken from the eyes as indicated in Fig. 2.

Male eye ratios vary from 1:0.5 (holoptic N. hudsoni) to 1:2.1 (dichoptic N. tonnoiri). The main disadvantage of the eye ratio is that it often necessitates the removal of the insect's head to allow a full-face view, as in Fig. 2., to be obtained.

The head-depth to head-width ratio is also used in descriptions of new material and has been calculated for existing species (Fig.2).

Genitalia: The terms dististyle and basistyle are used for the segments of the male genital forceps by Kitakami (1950), Stuckenberg (1958) and Alexander (1963). These two terms are used here in preference to those of clasper and basicoxite (Dumbleton 1963a). The term cercus (Stuckenberg 1958) is used for the bilobed extremity of the ninth tergite, rather than superior process (Dumbleton 1963a) (Fig. 19).

Because Stuckenberg (1958) apparently provided the first adequate account of the female genitalia of the Blepharoceridae and his terminology is used by Alexander (1963), his terms are used here whenever applicable i.e. oviscapt rather than subgenital plate (Dumbleton 1963a).

Pupa:

Pupae do not show any great generic or specific differences; however, Dumbleton (1963a) used the ratio of the basal width of the outer gill lamella to the length of the outer gill lamella to assist in identification (Fig. 3). This practice is continued here, but many pupae remain unidentified as the pupal gills are often too damaged by natural causes to be measured.

Larva:

Arbitrary terms have been used to designate the body segments of blepharocerid larvae by Tonnoir (1923c), Stuckenberg (1958) and Dumbleton (1963a) and their use is continued here (Fig. 1). The Cephalic Division includes the cephalic region, the three thoracic segments and the first abdominal segment and bears ventrally one sucker. The Median Divisions, five in number, represent single abdominal segments and bear suckers ventrally. The 5th median division (true 6th abdominal segment) is often almost completely fused to the Anal Division except for a lateral constriction. The Anal Division consists of four fused abdominal segments. Some of the confusion that existed over the number of segments fused into the Cephalic and Anal Divisions is discussed in Chapter II.

It is also shown in Chapter II, that the lateral abdominal projections of the larva are probably homologous with the embryonic thoracic prolegs. Therefore the term abdominal proleg is used for

such structures (Fig. 1) rather than the terms claw or fulcrum (Kitakami 1950), lateral process (Campbell 1923; Dumbleton 1963a), ambulatory process (Tonnoir 1930b) or pseudopod (Johannsen 1934; Stuckenberg 1958; Alexander 1963).

The term seta, defined by Stuckenberg (1958) as a "more or less flexible, slender pale, hair-like structure", is used here to describe small, clear, lanceolate, structures on the dorsal armature and on the ventral surface of the posterior margin of the larva (Fig. 48). The term spine as defined by Stuckenberg (1958) and as used by Dumbleton (1963a) for a dark rigid hair-like structure on the larva is also used (Fig. 53). The term scale is used for the clear fan-shaped structures that make up the marginal armature of Neocurupira larvae (Fig. 48).

Because the growth which takes place during each larval instar results in considerable changes in the proportions of the Cephalic and Median Divisions (e.g. first instar larva Figs. 43 & 44), descriptions are normally made from late larvae. In contrast, as Kitakami (1950) points out, the number of antennal segments, the shape of the abdominal prolegs, number of tracheal gills, hair length and sucker size remain constant throughout any one instar. These structures are all useful as diagnostic characters.

The sucker approximately doubles in size with each ecdysis and in New Zealand blepharocerids, as with some other blepharocerids, can be used to identify instars. The differences in size of suckers during any one instar can be used to some extent to identify species

of larvae.

As fixation of the larva causes the suckers to become slightly oval in shape, the sucker width is taken as the greatest measurement across the sucker (normally at right angles to the long axis of the larva).

CLASSIFICATION.

At present the family Blepharoceridae is divided into four subfamilies (Kitakami 1950, Alexander 1958 and 1963), Edwardsininae Edwards (1929), Blepharocerinae Bezzi (1912), Paltostominae Bezzi (1912), and Apistomyiinae Bezzi (1912). This division, which is used here, is based primarily on the wing venation and the head structure of the adults.

Stuckenburg (1958) believes that the family should be primarily divided into Edwardsininae and Blepharocerinae, and that because the present Blepharocerinae, Paltostominae and Apistomyiinae are not of equal rank either one with another, or with the Edwardsininae they should be reduced to the status of tribes within the Blepharocerinae.

On the basis of wing venation (M_3 and m-cu both absent) and mouthpart structure (labial palpi long and slender), all known N.Z. Blepharoceridae belong to the subfamily Apistomyiinae.

NEOCURUPIRA Lamb 1912

Neocurupira Lamb, 1912. Trans. N.Z. Inst. 45: 72-73.

Type species N. hudsoni.

N. (Neocurupira), Edwards, 1929. Brit.Mus. (Nat.Hist). pt. 2, fasc, 2: 75; Alexander, 1958. Proc. 10th Int. Congr. Ent. (1956), 1: 813-824; Dumbleton, 1963, N.Z. Jour. Sci. 6, 2: 234-258.

Paracurupira Tillyard, 1922. N.Z. Sci.Tech. 5: 101-107.

Type species Curupira chiltoni Campbell (1921).

NEW SYNONYMY.

N. (Paracurupira), Edwards, 1929. Brit. Mus. (Nat.Hist.). pt.2, fasc. 2: 75; Alexander, 1958. Proc. 10th Int. Congr. Ent. (1956), 1: 813-824; Dumbleton, 1963. N.Z. Jour. Sci. 6, 2: 234-258.

(Note: The affinities of the subgenus N. (Austrocurupira) Dumbleton 1963a,(type species Neocurupira nicholsoni Tillyard) are doubtful but its present position is tentatively accepted here.)

The hudsoni-complex

The present distribution of Neocurupira hudsoni, based on collections of holoptic eyed males, extends from the Marlborough Sounds in the north of the South Island, southwards along the Southern Alps to a boundary which extends east from Lake Wanaka through the Nevis River Gorge, across the Umbrella Mountain Range to near Roxburgh (Fig. 26). Throughout this area of distribution there is no significant morphological variation in either adults, pupae or larvae.

Blepharocerids found to the south of the area of distribution of N. hudsoni are, in the larval stages morphologically indistinguishable from N. hudsoni, but the adult males possess dichoptic eyes. These blepharocerids will be referred to as the "southern" forms and described as Forms A, B, C and D; for reasons discussed later (p.31) they are here placed along with N. hudsoni in the hudsoni-complex, but are not given any further taxonomic status.

Full descriptions are given for Forms B and D as it is considered that these forms may eventually be raised to specific status. Because Form A is probably conspecific with N. hudsoni and Form C appears to be the hybrid of N. hudsoni and Form D they are not described fully.

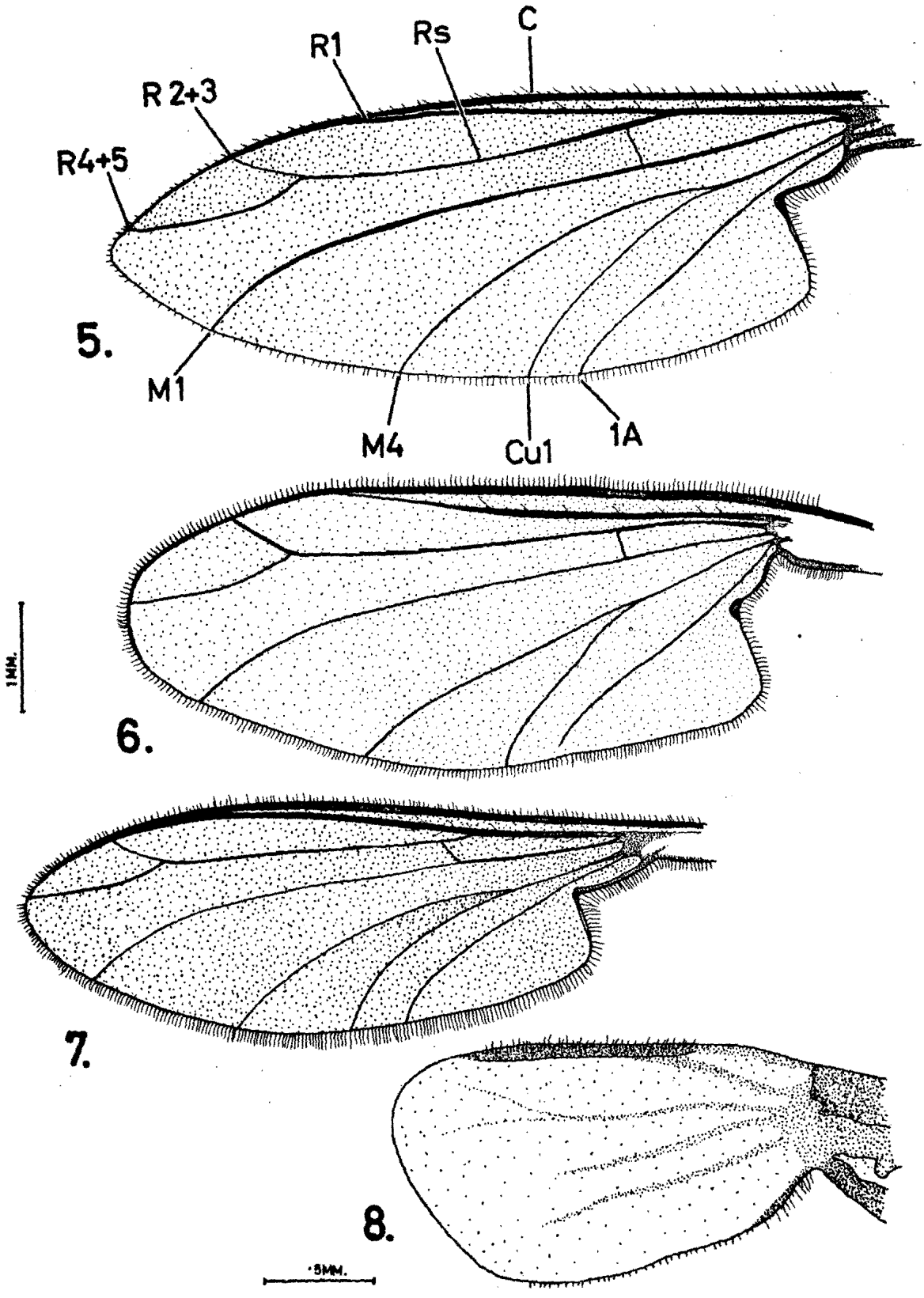
Figures:-

5. Macropterous wing of N. hudsoni male.

6. Wing of Form B male.

7. Wing of Form D male.

8. Brachypterous wing of N. hudsoni male.

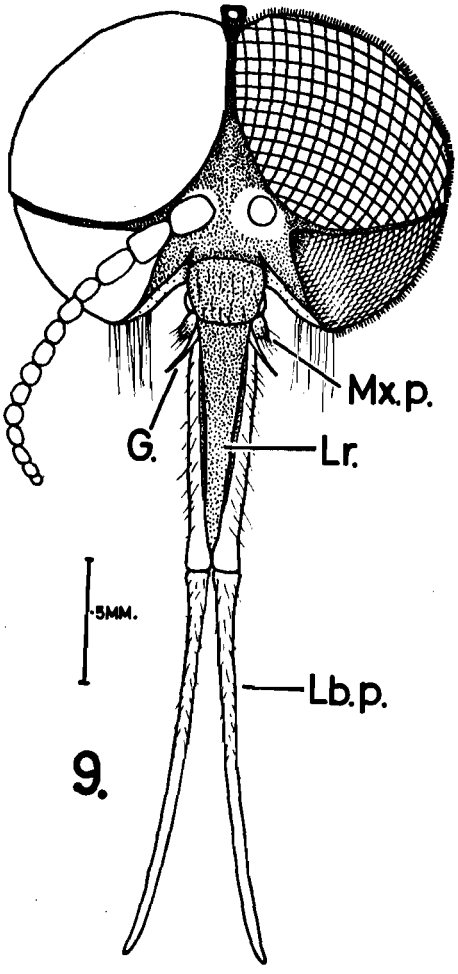

C
Rs
R1
R 2+3
R4+5
M1
M4
Cu1
1A
5.
6.
7.
8.
1MM.
5MM.

Figures:-

9. Frontal view of head of N. hudsoni male.
10. Frontal view of head of Form C male.
11. Oviscapt of N. hudsoni female.
12. Oviscapt of Form B. female.
13. Oviscapt of Form D. female.

Abbreviations:-

G.	-	Galea.
Lb. P.	-	Labial palp.
Lr.	-	Labrum.
Mg. 8th. t.	-	Margin of 8th tergite.
Mx. p.	-	Maxillary palp.
Ovt.	-	Oviscapt.



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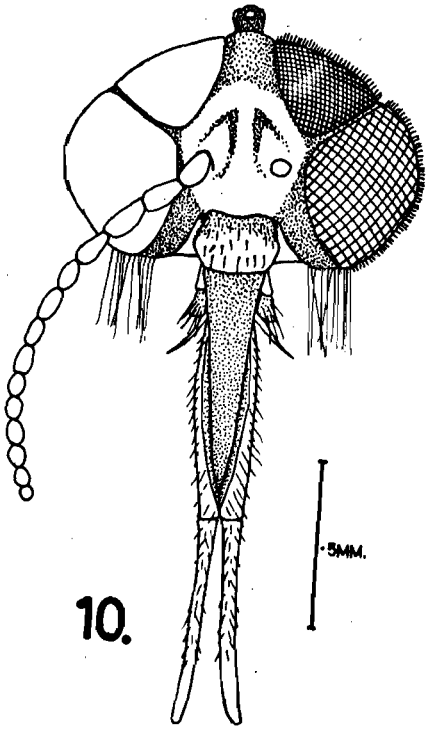

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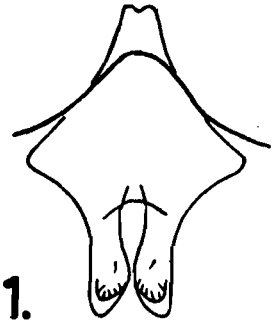

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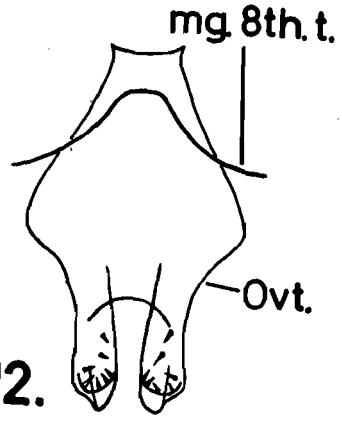

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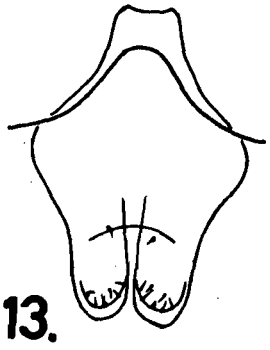


13.

·25MM.

Neocurupira (N) hudsoni Lamb

Neocurupira hudsoni Lamb, 1912. Trans. N.Z. Inst., 45: 70-75;
Campbell, 1921, Trans. N.Z. Inst., 53: 258-266.
N. (N) hudsoni, Tillyard, 1922, N.Z. J. Sci. Tech., 5: 101-107;
Dumbleton, 1963, N.Z. J. Sci. 6, 2: 234-258.

Adult.

Male. Body length 9.5-11.0 mm.

Head. (Fig. 9). Depth width ratio 1:1.3; eyes holoptic, eye ratio 1:0.5, upper facets large; labial palpi twice as long as head depth; 10-11 lateral facial hairs.

Normal wing (Fig. 5). Length 7.2-10.0 mm.

Brachypterous wing (Fig. 8). Length 2.5 mm.

Genitalia. Median concavity of cercus variable but notched basally, lateral lobes variable (Figs. 18 and 21); dististyles broad basally, widest at midlength (Fig. 18).

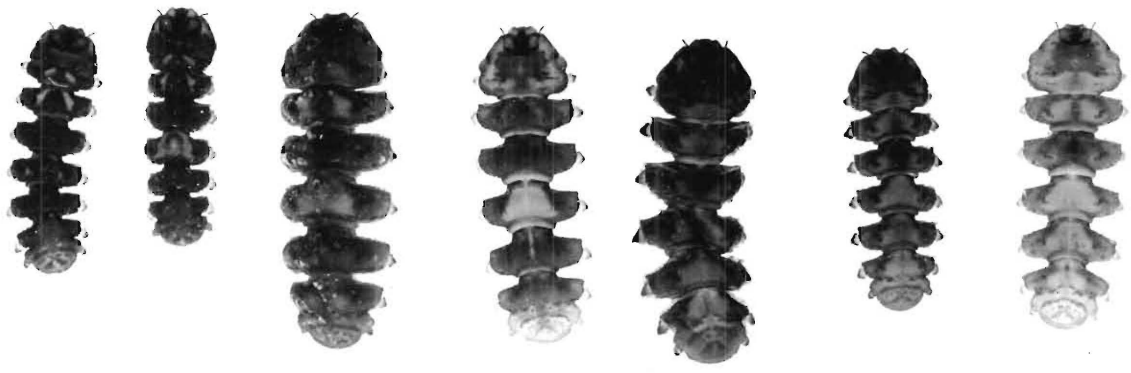
Female. Body length 5.5-8.0 mm.

Head. Depth width ratio 1:1.3; eyes dichoptic; eye ratio 1:1.6; labial palpi 1.5 times as long as head depth; vertex area keel-like and 0.25 times as wide as head width.

Wing. More membranous than male wing, length 7.2-9.0 mm.

Genitalia. (Fig. 11). Internal process of oviscapt truncate, slightly concave apically, oviscapt lobes bearing 6-7 dark spines sub-apically.

a



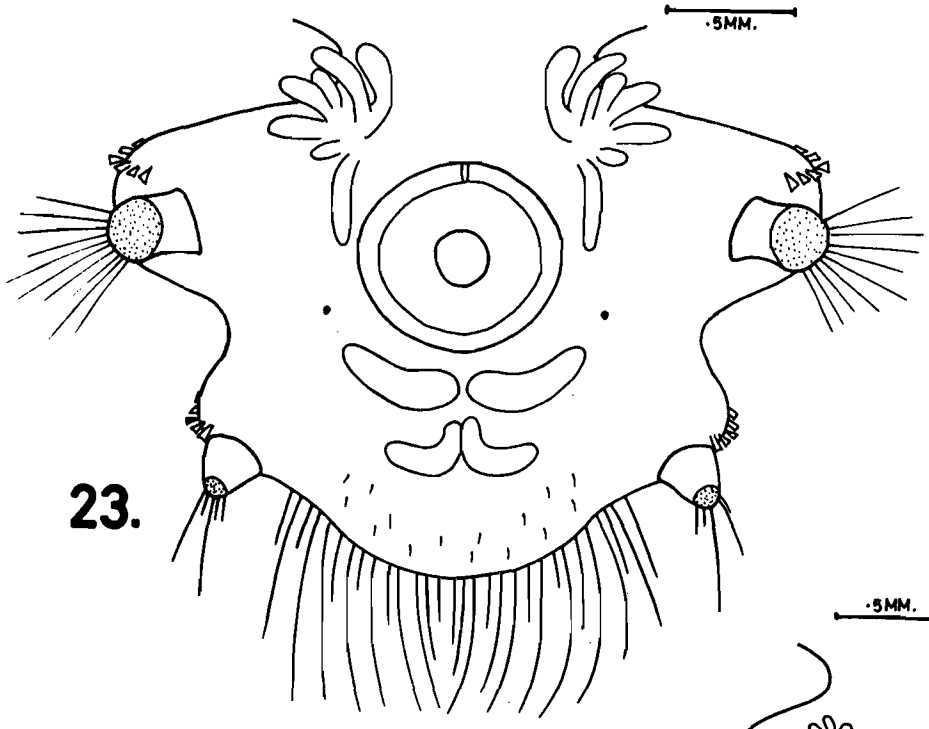
b

Chapter I

Plate 1.

(a) A series of *N.hudsoni* fourth instar larvae showing range in colour pattern.

(b) A series of *N.tonnoiri* fourth instar larvae showing range in colour pattern.



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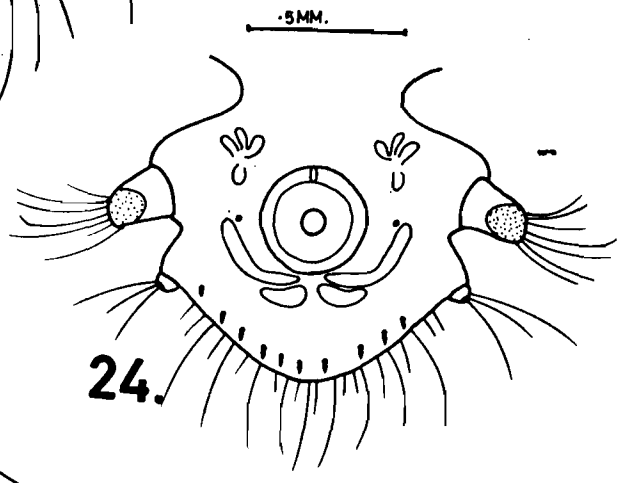

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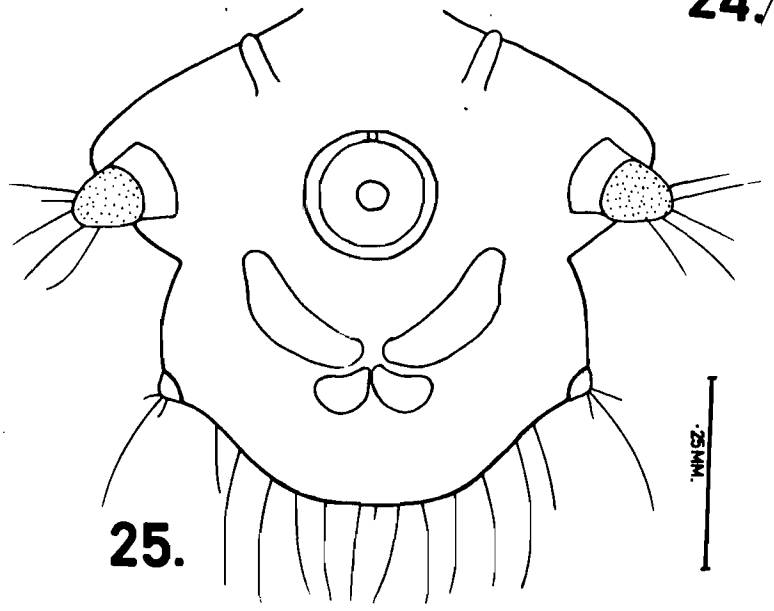


25.

Figures:-

23. Ventral view of posterior end of N. hudsoni fourth instar larva.

24. Ventral view of posterior end of N. hudsoni third instar larva.

25. Ventral view of posterior end of N. hudsoni second instar larva.

Pupa. Length 6-8 mm.

Outer lamellae of pupal gills tapering, broadly rounded apically, basal width length ratio 1:2.7; inner lamellae shorter than outer lamellae.

Larva.

Fourth instar (Fig. 23). Length 5.9-14.0 mm. Sucker width 0.60-0.89 mm. Colour of the cephalic sclerites varying from moderate yellowish orange (10YR7/6) mottled with dusky brown (5YR2/2) (early) to black (N1) (late) (Plate 1a).

Colour of remainder of body is variable from uniform light brown (5YR5/6) to moderate brown (5YR3/4). Colour pattern varying from uniform light brown with triangular  pale yellowish orange (10YR8/6) patch on dorsum of 3rd median division, or uniform light brown with lateral lunar markings of greyish yellow (5Y8/4) on all divisions, to completely greyish yellow except for light brown markings on 2nd division and on anterior region of other median divisions; abdominal prolegs rounded apically, not angulate laterally; posterior margin of anal division bearing approximately 30 hairs.

Third instar (Fig. 24). Length 3.4-4.5 mm. Sucker width 0.35-0.50 mm. Colour of cephalic sclerites varying from light brown (early), to dusky brown (5YR2/2) (late); colour of remainder of body uniform but varying from moderate brown (5YR3/4) to light brown (5YR5/4); cephalic sclerites occupying 2/3 (early) and 1/3 (late) length of

the cephalic division; marginal armature of white cone-shaped scales; dorsal armature of short setae irregularly arranged at approximately two seta lengths apart; dorsal cuticle microsculptured into ridges and grooves; lateral edges of median divisions subangulate; abdominal prolegs 1/5 longer than basal width, subangulate apically, very slightly constricted medially, bearing dorsally short hairs plus 7 fine hairs as long as proleg, ventral pad 1/2 as long as proleg; seventh abdominal proleg slightly shorter than basal width, bearing 2-3 hairs 3 times as long as proleg; anal division separated laterally from fifth median division by subangulate constriction; posterior margin of anal division broadly rounded bearing 7-9 irregularly arranged hairs, each as long as hairs on 7th proleg, as well as 12-14 shorter hairs and 10-12 setae ventral to posterior margin; eight tracheal gill filaments per division; anterior anal gill filaments large, partly encircling sixth sucker.

Second instar (Fig. 25). Length 2.8-3.4 mm. Sucker width 0.19-0.24 mm. Colour of cephalic sclerites dusky brown (5YR2/2); remainder of body uniformly light brown (5YR5/4); cephalic sclerites occupying ⅓ (early) to 1/5 (late) length of cephalic division; marginal armature anteriorly 11 scales per division, posteriorly 4 scales per division; dorsal armature not apparent; lateral margins of median divisions subangulate anteriolaterally, slightly rounded posteriolaterally; abdominal prolegs as long as basal width

rounded apically, slightly constricted medially, bearing dorsally 5 hairs each as long as proleg, ventral pad 1/3-1/2 as long as proleg; seventh proleg wider than long, bearing one hair 4-5 times as long as proleg plus two smaller hairs, no apparent ventral pad; anal division separated laterally from fifth median division by broady angulate constriction; posterior margin of anal division broadly rounded medially, slightly concave laterally bearing 12-13 hairs as long as 7th proleg hair; two tracheal gill filaments per division; posterior anal gill filaments 1/3-1/2 size of anterior filaments.

Locality Records.

Red Pine (Pouawhariki) Gully, Moncrieff Scenic Reserve, Croiselles Bay, Marlborough Sounds, S15. 995483., L.P., V.M.S., 30, D.A.C., ?-xii-65, Cant. Mus.;

Wangamoa River, Nelson, S14. 798367., L.A., W.P.Thomas, 22-xii-63, D.A.C., 21-xii-62, 31-xii-62, 1-i-65, Cant. Mus; annon.,3-ii-64, Uni. Auck.;

Maitai River, Nelson, L.P., L.J.D., 23-i-50, 23-i-54, Ent.Div.L., S20. 683262., D.A.C., 27-xii-62, Cant. Mus.;

Brook Stream Reservoir, Nelson, S20. 638236., L., D.A.C., 30-xii-64, Cant. Mus.;

Marsden Valley, Stoke, S20. 617217., L.P., D.A.C., 24-xii-62, 1-i-64, Cant. Mus.;

Lee River, Brightwater, S20. 516114., L., D.A.C., 25-xii-62, Cant. Mus.;

Buller River Bridge, Lake Rotoiti, S33. 193680., L., L.J.D., 10-i-60, Ent. Div. L;

Travers Valley, Lake Rotoiti, L., B.M.Fitzgerald, 1964, Cant. Mus;

Hopeless Creek, Travers Valley 2400 ft., L.P. J.Flux, 10-ii-65, Cant. Mus;

Sabine River, Lake Rotoroa, L., L.J.D., ?-x-50, Ent. Div. L;

Puhi Puhi, Kaikoura, L.J.D., 6-i-60, Ent. Div. L;

Mount Fyffe, Kaikoura, L.J.D., 14-v-62, Ent. Div. L;

Boyds Creek, Kaikoura, S49. 890988., L.P.A., D.A.C., 29-viii-62, 31-xii-62, Cant. Mus.;

Kowhai River, Kaikoura, L.P., 150'., S49. 909936., V.M.S., 2-ix-64, (142), D.A.C., 19-ix-64, Cant. Mus., 1100ft., S49. 868019., ?-i-66, Cant. Mus.;

Jack's Pass, Hamner, L., L.J.D., 12-v-54, Ent. Div. L;

Waterfall Stream, Lake Taylor, L., F.R.Allison, 14-i-64, Cant.Mus;

Rough Creek, Lewis Pass, L.P., D.A.C., 12-ii-62, Cant.Mus.;

Unnamed Creek, Lewis Pass, L.P., D.A.C., 12-ii-62, Cant.Mus.;

Mount Arthur, Nelson, A., A.Philpott, 22-xii-21, Ent. Div. N;

Cobb River, Takaka, 2500ft., L., S.G.Moore, 4-iv-65, Cant. Mus;

Fossil Creek & Brown River, Heaphy Track, L.P., J.Grieve & M.Cross, 10-i-65, Cant.Mus;

Gouland Downs, Heaphy Track, A.L.Tonnoir, (1923b);

Barrytown Beach, Barrytown, Greymouth, 10ft., L.P., A.G.McFarlane, 17-xii-63, Cant. Mus;

13 Mile Creek, Greymouth, L., L.J.D., 11-i-60, Ent. Div. L; Annon, 28-i-66, Uni. Auck.;

Wanganui River, West Coast, L.P., V.M.S., 12-x-61, 206;

Waikukupa River, West Coast, L.J.D., Ent. Div. L.;

Clearwater River, Fox, P., D.A.C., 9-ii-66, Cant. Mus.;

Otira, A., A.L.Tonnoir, 16-ii-22, Ent. Div. N., T. Harris, Cant. Mus.;

Warnocks Nob, Otira, A., G.V. Hudson, 13-xii-08, Dom. Mus.;

Otira Valley, S59. 050337., D.A.C., 19-i-63, 23-ii-63, Cant. Mus.;

Pegleg Creek, Arthur's Pass, S59. 055340., L.P.A., L.J.D., 30-i-60, Ent. Div. L.; D.A.C., 15-xii-62, Cant. Mus.;

Temple Basin, 5000 ft., L., L.J.D., 31-i-58, Ent. Div. L.;

Twin Creek, S59. 053322., L.,D.A.C., 29-vii-62, Cant. Mus.;

Bealey Glacier, Mount Rolleston, S59. 027318., 4250 ft., L.P., Sykes, 9-ii-63, Ent. Div. L., D.A.C., 3-ix-63, Cant. Mus.;

Bealey Chasm, Bealey River, S59. 050313., 2750 ft., D.A.C., 1962-1966, Zoology Department, University of Canterbury;

McGraths Creek, S59. 053300., L.P., D.A.C., 29-vii-62, Cant. Mus.; A.G.McFarlane, 31-i-65, Cant. Mus.;

Punch Bowl, S59. 055295., 2500 ft., L., D.A.C., 20-i-62, 20-i-63, Cant. Mus.;

Bealey River, A., G.V.Hudson, 10-ii-20, Dom. Mus.;

Arthur's Pass, A., A.L.Tonnoir, 18-i-20, Ent. Div. N., Annon., ?-xii-22, Dom. Mus.;

Snow Creek, S59. 065264., L.P., D.A.C., 28-iv-63, Cant. Mus.;

Halpin Creek, S59. 070244., L., L.J.D., 13-iv-62, Ent. Div. L.;

Mingha River, S59. 114297., L.P., D.A.C., 16-xii-63, Cant. Mus.;

Andrews Stream, Hallelujah Flats, S59. 280167., L.A., 14-xi-64,D.A.C., Cant. Mus.;

Linwood Creek, Minchin River, S59. 278446., L.P.A., D.A.C., 18-iv-65, Cant. Mus.;

Sudden Valley, Hawdon River, L., S59. 195244., D.A.C., 19-iv-64, Cant. Mus.;

Betwixt Stream, Cass, S66. 201172., L., D.A.C., 18-iv-64, Cant. Mus.;

Ribbon Wood Creek, Cass, L., E. Percival, 20-x-33, (Misc.);

West Cass River, S66. 193124., L., D.A.C., 13-xi-64, Cant. Mus.;

Cass River, S66. 211161., L.P., D.A.C., 24-iii-62, Cant. Mus.;

Cass, A., A.L.Tonnoir, ?-ii-25, Cant. Mus.;

Masons Creek, Flock Hill, Craigieburn Mountain Range, 3800 ft., A., P.M.Johns, 21-i-65, Cant. Mus.;

Ryton River, Lake Coleridge, S74. 053898., D.A.C., 10-ii-63, Cant.Mus.;

Mount Hutt, 2500 ft., P.A., G.Tunnicliffe & W.P.Thomas, 29-i-64, Cant. Mus.;

Taylor Stream, Ashburton River, L.P., D.A.C. & V.M.S., 27-i-64, (123);

Moa River, Wilberforce River, L., D.A.C., 19-x-63, (1);

Kiwi River, Wilberforce, 2000 ft., L.P., D.A.C., 19-x-63, Cant.Mus.;

East Kiwi River, L., D.A.C., 19-x-63, (2);

Kakapo River, Wilberforce, L., D.A.C., 19-x-63, (4);

East Kakapo River, 3000 ft., L., D.A.C., 18-x-63, Cant. Mus.;

Lower Kakapo River, 2000 ft., L.P.A., D.A.C., 18-x-63, Cant. Mus.;

Godley Hut, Godley Glacier, L.J.D., 11-xii-58, Ent. Div. L.;

Jacks Stream, Mount Cook, L., D.R.C., 24-i-65, Uni. Auck.;

Bush Stream, Mount Cook, S89. 773155, L.J.D., 14-x-58, Ent. Div. L; D.A.C. & V.M.S., 11-i-64, (61);

Black Birch Stream, Mount Cook, S89. 760300., L.P., D.A.C. & V.M.S., 9-i-64, (59 & 59a);

Lake Ohau, 1720 ft., L., P.M.Johns, 13-x-63, Cant. Mus.;

Parson's Rock Stream, Otematata, L.P., D.A.C. & V.M.S., 24-i-64, (108); D.A.C., 29-ii-64, Cant. Mus.;

Shingle Creek, Roxburgh, L.P.A., D.A.C. & V.M.S., 21-i-64, (97);

Neck Creek, Lake Hawea, 1325 ft., L.P.A., D.A.C., 13-i-65, Cant.Mus.;

Sawyer's Burn, Lake Hawea, 1325 ft., L., D.A.C., 26-x-64, Cant. Mus.;

Camp Stream, Lake Wanaka, 930 ft., L.P., D.A.C. & V.M.S., 12-i-64, (68);

Boundary Creek, Lake Wanaka, 1000 ft., D.A.C. & V.M.S., 12-i-64, (69);

Camerons Creek, Makarora River, L.P., D.A.C. & V.M.S., 12-i-64, (71); D.A.C., 27-x-64, (197);

Brady Creek, Makarora River, L., D.A.C. & V.M.S., 12-i-64, (70);

Roaring Swine River, Haast River, 160 ft., L., D.A.C. & V.M.S., 14-i-64, (78).;

Harris Creek, Haast River, L., D.A.C. & V.M.S., 14-i-64, (77);

McPherson's Creek, Haast River, L.A., D.A.C. & V.M.S., 14-i-64, (79);

Gates of Haast, Haast River, L.P.A., D.A.C. & V.M.S., 14-i-64, (80); D.A.C., 27-x-64, (195);

Pyke Creek, Haast River, L., D.A.C. & V.M.S., 14-i-64, (81);

Haast River, 1550 ft., L.P., D.A.C., 27-x-64, (196);

Camp Creek, Haast River, 980 ft., D.A.C., 27-x-64, (199);

Phoebe Creek, Matukituki River, Lake Wanaka, P., D.A.C., 8-ii-66 Cant. Mus.;

Old Homestead Creek, Matukituki River, 1400 ft., D.A.C., 26-x-64, (190), 8-ii-66, Cant. Mus.;

Bridal Veil Falls, Matukituki River, 1400 ft., D.A.C., 12-i-65, Cant. Mus.;

Raspberry Hut Stream, Matukituki River, P.A., D.A.C., 8-ii-66, Cant. Mus.;

Lumberbox Creek, Lake Wakatipu, 1100 ft., L.P., D.A.C. & V.M.S., 15-i-64, (83); D.R.C., 29-i-65, Uni.Auck.;

Nevis River Gorge, Nevis Valley, Lake Wakatipu, L P., D.A.C., 7-ii-66, Cant. Mus.;

Piano Flat, Whakæea River, Southland, L.J.D., Ent. Div. L.

Neocurupira hudsoni is the only New Zealand species of blepharocerid possessing truly holoptic eyes in the male adult. In this regard it is similar to the adult male of the Australian Neocurupira nicholsoni. The wing venations of these two species are also very similar (Tillyard, 1922b).

The wings of N.hudsoni adults, in particular those from south of Mount Cook and occasionally from elsewhere, show a reduction in the thickness of vein R2+3 and an increase in the thickness of vein R4+5 (Fig. 5). Specimens have been collected where the vein R2+3 is considerably reduced and not immediately obvious as is normal.

N. hudsoni has the widest distribution of any New Zealand blepharocerid and occurs mainly in open, stable streams and rivers, having a good flow of water, with an altitudinal distribution from just above sea level to 5000 ft. (Fig. 26). It is often found associated with the other South Island blepharocerids when the areas of distribution coincide.

The commensal chironomid Dactylocladius commensalis Tonnoir occurs with the larvae of N.hudsoni throughout their area of distribution.

FORM A

Adult (Dissected from pupae)

Male. Body length 7.9-9.0 mm.

Head as for N. hudsoni; labial palpi from 1.2-1.7 times as long as head depth; 4-5 lateral facial hairs.

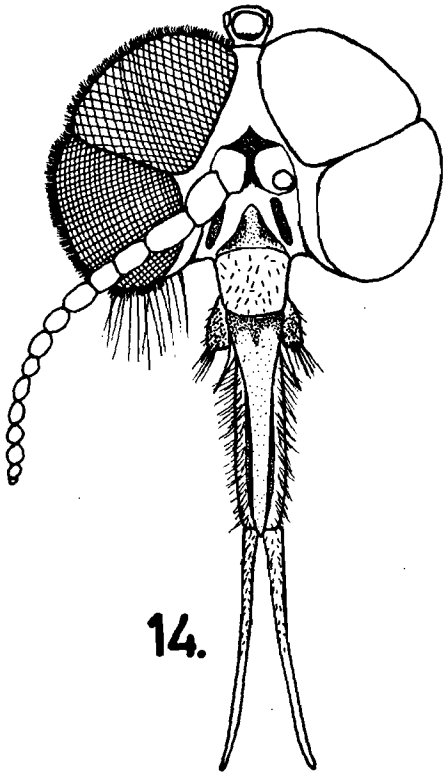
Genitalia. As for N. hudsoni.

Female. Similar to N. hudsoni females.

Larva. Not known.

Locality record. Otago, P, collector unknown, Cant. Mus.

Apart from the short labial palpi and fewer lateral facial hairs of the male, Form A is very similar to and probably conspecific with N. hudsoni. Form A is placed in the same series as the "southern" forms because the location is unknown and it possesses short labial palpi similar to Forms B, C, D.



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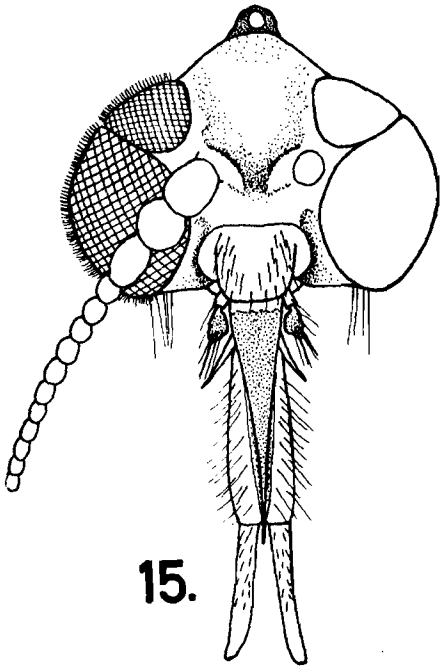

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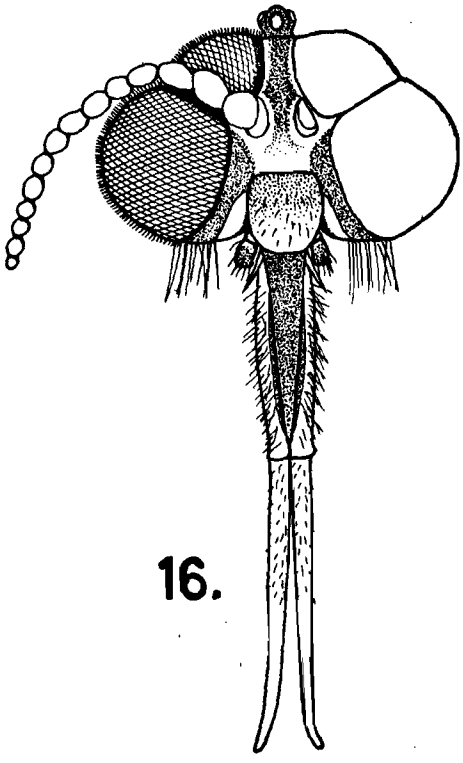

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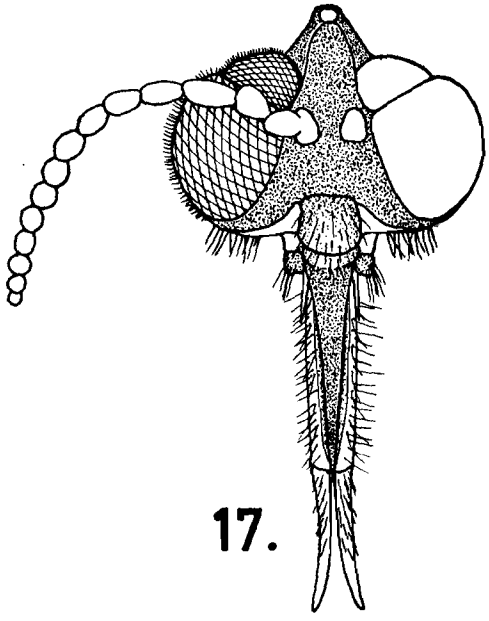

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Figures:-

14. Frontal view of head of Form B male.

15. Frontal view of head of Form B female.

16. Frontal view of head of Form D male.

17. Frontal view of head of Form D female.

FORM B.

Adult.

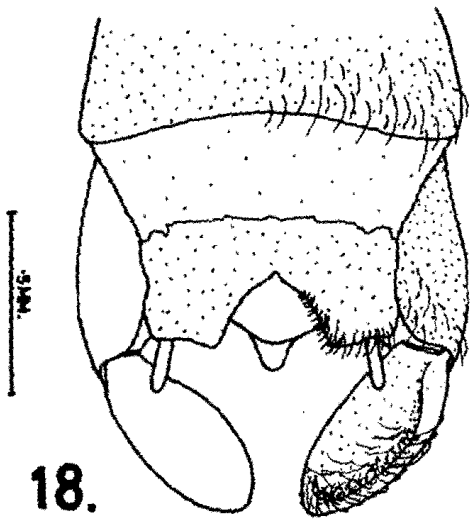
Male. (Dissected from pupae) Body length 6.6-7.3 mm.

Head. (Fig. 14). Globular; colour moderate yellowish brown (10YR5/4); depth width ratio 1:1.5; eyes dichoptic, eye ratio 1:0.9, upper facets slightly larger than lower facets, eye margins contiguous; vertex area 0.06 times as wide as head-width; ocellar turret prominent, anterior ocellus prominent; antennae 14-segmented, 5 proximal segments longer than wide, remainder moniliform; clypeus as long as wide, colour pale yellowish orange (10YR8/6), darker on proximal border, bearing 20-24 short, black hairs; labrum darker than clypeus, with heavily pigmented proximal border, shorter than head depth, slightly longer than proximal segment of labial palpi; maxillary palpi two-segmented, proximal segment small, distal segment black, truncated, bearing anteriolaterally 17-19 black hairs; galea prominent 0.66 times as long as maxillary palp; labial palpi twice as long as head depth, distal segments diverging; 15-17 lateral facial hairs.

Thorax. As for N. hudsoni.

Wing. (Fig. 6). Length 7.5-8.1 mm. Venation similar to N. hudsoni, wing apex rounded.

Genitalia. (Fig. 19). Posterior lateral margin of cercus



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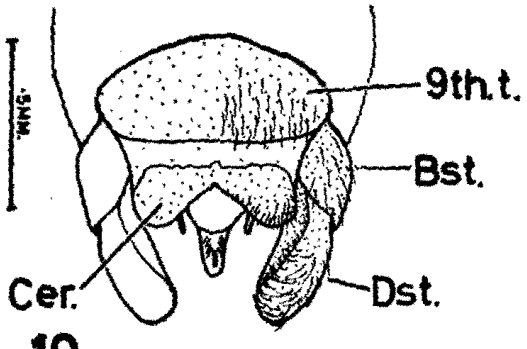

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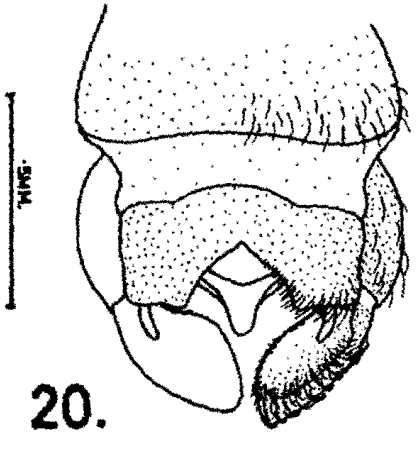

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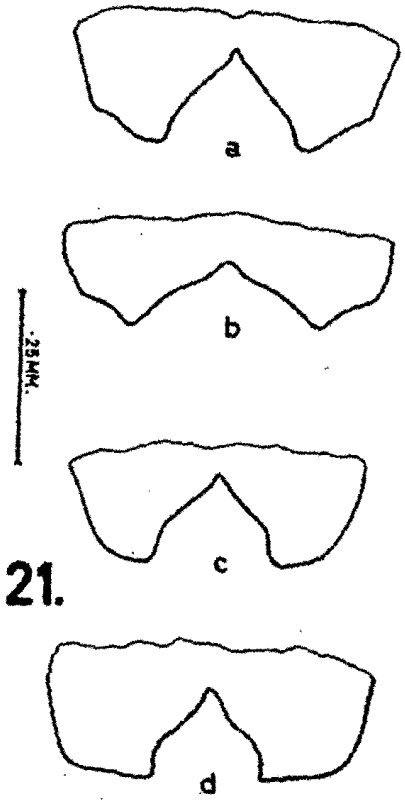

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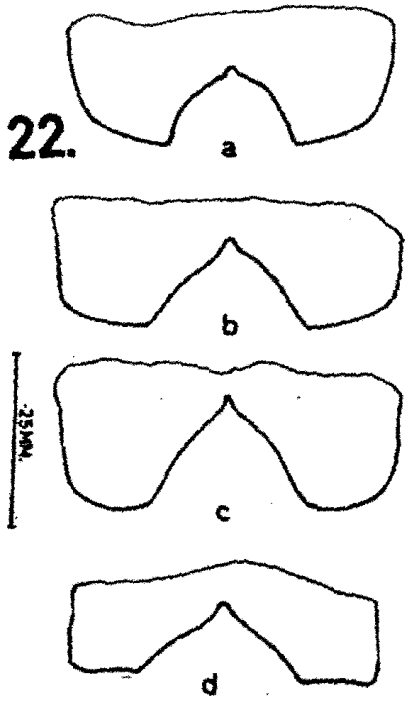


22.

Figures:-

18. Dorsal view of N. hudsoni male genitalia.

19. Dorsal view of Form B male genitalia.

20. Dorsal view of Form D male genitalia.

21. Variation in shape of the cercus of N. hudsoni males.

22. Variation in shape of the cercus of Form D males.

Abbreviations:-

Bst.	-	Basistyle.
Cer.	-	Cercus.
Dst.	-	Dististyle.
9th. t.	-	9th tergite.

rounded, median concavity notched basally, sides straight to slightly concave; dististyles as for N. hudsoni. (The apparent differences obvious in Fig. 19 are due to the drawing being taken from an adult dissected from the pupa).

Female. (Dissected from pupa). Body length 8.4 mm.

Head. (Fig. 15). Colour as for male; depth width ratio 1:1.2; eyes dichoptic, eye ratio 1:1.8; upper facets slightly smaller than lower facets; vertex area 0.33 times as wide as head-width, only slightly protruding anteriorly from eye level; ocellar turret raised, base diverging, anterior ocellus prominent; antennae 14-segmented, moniliform, proximal three segments larger than rest; clypeus wider than long, colour pale yellowish orange (10YR8/6), bearing 23-25 short, black hairs; labrum darker than clypeus, with lighter coloured proximal border, longer than proximal segment of labial palpi, finely tapering; maxillary palpi two segmented, distal segment larger, constricted basally, angulate distolaterally, bearing 11-13 black hairs; galae prominent, twice as long as maxillary palp; labial palpi 1.5 times as long as head depth, distal segment short; 4-5 lateral facial hairs.

Thorax. As for N. hudsoni.

Wing. Venation and shape similar to male, length 8.1 mm.

Genitalia. (Fig. 12). Internal process of oviscapt tapering, apex shallowly concave, oviscapt lobes bearing 7-8 short, clear spines subapically.

Pupa. Length 7.0-8.7 mm. Width 3.1-3.8 mm. Similar to N. hudsoni

Basal width length ratio of outer lamellae 1:2.5.

Larvae. Similar in all stages to N. hudsoni.

Locality Records.

Shepards Stream, Waipouri Falls, Dunedin S163 708666., approx. 800ft., L.& P., D.A.C. 18-x-64, (167), C.Devine, 8-xi-64, Cant. Mus.; Post Office Stream, Mount Maungatua, Dunedin S163 767750., 1000ft.approx. L. & P., D.A.C., 18-x-64, (164), 5-ii-66, Cant. Mus.

Form B is to date known only from a restricted area near Dunedin (Fig. 26). The adult male exhibits an interesting eye structure (Fig. 14), which is intermediate between the holoptic condition, of N. hudsoni and the dichoptic condition of Form D. The labial palpi are shorter than those of N. hudsoni, and the wing, though similar in venation, is more bluntly rounded apically. Apart from these differences the genitalia and body of the male adult are very similar to those of N. hudsoni. The female Form B shows considerable differences in head structure from the females of N. hudsoni and of Form D. The vertex area is wider and more rounded dorsally and does not protrude greatly above the level of the eye as it does in the typical N. hudsoni female. The distal segments of the maxillary palp and the galea are more prominent than in N. hudsoni.

The oviscapt (Fig. 12) of the female genitalia shows a mixture of characters similar to those shown by the oviscapts of N. hudsoni

and of Form D. The distal lobes are more similar to those of N. hudsoni (Fig. 11), but the internal process is more similar to that of Form D (Fig. 13). The subapical spines are clear, in contrast to those of both N. hudsoni and Form D which are black.

The larvae associated with the pupae of Form B are highly patterned, similar to the other larvae of the hudsoni-complex, and are morphologically indistinct from N. hudsoni larvae.

The commensal chironomid Dactylocladius commensalis Tonnoir has not as yet been found associated with the larvae of Form B.

FORM C.

Adults.

Male. Head (Fig. 10). Depth width ratio 1:.77; eyes dichoptic, eye ratio 1:1.2, upper and lower eye not contiguous; vertex slightly raised, 0.17 times as wide as head width; maxillary palpi as long as labrum; galea as long as maxillary palp; labial palpi 1.7 times as long as head depth; 10-11 lateral facial hairs.

Body. Similar to N. hudsoni

Female. Not known.

Locality Records.

Raspberry Hut Stream, Matukituki Valley, Lake Wanaka, 1500 ft., D.A.C., 8-ii-66, Cant. Mus.;

Motatapu Gorge, Lake Wanaka, approx. 950 ft., D.A.C., 9-ii-66, Cant. Mus.

Form C has only been found in populations containing both N. hudsoni and Form D (Fig. 26). The shape of the head and ocellus, and the non-contiguous eye margins are more similar to those of N. hudsoni, while the eye ratio and the proportions of the mouth parts are more similar to those of Forms B and D.

Because Form C is known only to occur with N. hudsoni and Form D, and shows a mixture of head characteristics of these associates, it is considered here to be the hybrid of N. hudsoni and Form D.

FORM D

Adult.

Male. Body length 6.8-8.0 mm.

Head (Fig. 16). Trapezoidal; colour varying from dusky yellowish brown (10YR2/2) to brownish black (5YR2/1); depth width ratio 1:1.5; eyes dichoptic, eye ratio 1:1.5, upper and lower facets equal in size, eye margins contiguous, black unfaceted peripheral band around upper eye; vertex area 0.1 times as wide as head-width; ocellar turret raised, constricted basally; antennae 14-segmented, moniliform; clypeal margin of frons light in colour, lateral areas darker; clypeus as long as wide, distal edge lighter in colour, bearing 16-20 short black hairs; labrum black, slightly shorter than proximal segment of labial palpi; maxillary palpi two-segmented, distal segment larger and black in colour, bearing anterolaterally 18-20 black hairs; galea twice as long as distal segment of maxillary palp; labial palpi 2.2 times as long as head-depth, distal segment slightly longer than clypeus plus labrum, diverging; 10-12 lateral facial hairs.

Thorax. As for N. hudsoni.

Wing (Fig. 7). Similar in shape and venation to N. hudsoni but not in length 6.2-7.3 mm.

Genitalia. Posterior lateral margin of cercus variable (Figs. 20 and 22), but median concavity always notched basally (as in N. hudsoni); dististyles as for N. hudsoni (Fig. 21).

Female. Body length 7.0-7.9 mm.

Head. (Fig. 17). Globular; colour brownish black (5YR2/1); depth width ratio 1:1.3; eyes dichoptic, eye ratio 1:2.8, upper facets smaller than lower facets; vertex area 0.17 times as wide as head width, protruding above eye level to form keel-like structure; ocellar turret raised, prominent, base diverging; antennae 14-segmented; clypeus as long as wide, dark with distal dusky yellow (5Y6/4) edge, bearing 16-20 short black hairs; labrum black, slightly longer than proximal segment of labial palp; maxillary palpi two segmented, segments of equal size, distal segment black, bearing anteriolaterally 8-10 black hairs; galea twice as long as maxillary palp; labial palpi 1.5 times as long as head-depth, distal segments short; 10-14 lateral facial hairs.

Thorax. As for male.

Wing. Length 8.0-9.1 mm. As for male but more membranous and junction of vein A1 to margin very weak.

Genitalia (Fig. 13). Internal process of oviscapt constricted laterally, shallowly concave apically, oviscapt lobes bearing 6-8 short black spines subapically.

Pupa. Length 5.8-6.4 mm. Width 2.5-2.9 mm.

Similar to N. hudsoni. Basal width length ratio of outer gill lamellae 1:3.0, sides of posterior outer lamellae gradually tapering, apex rounded; middle lamellae longer and wider

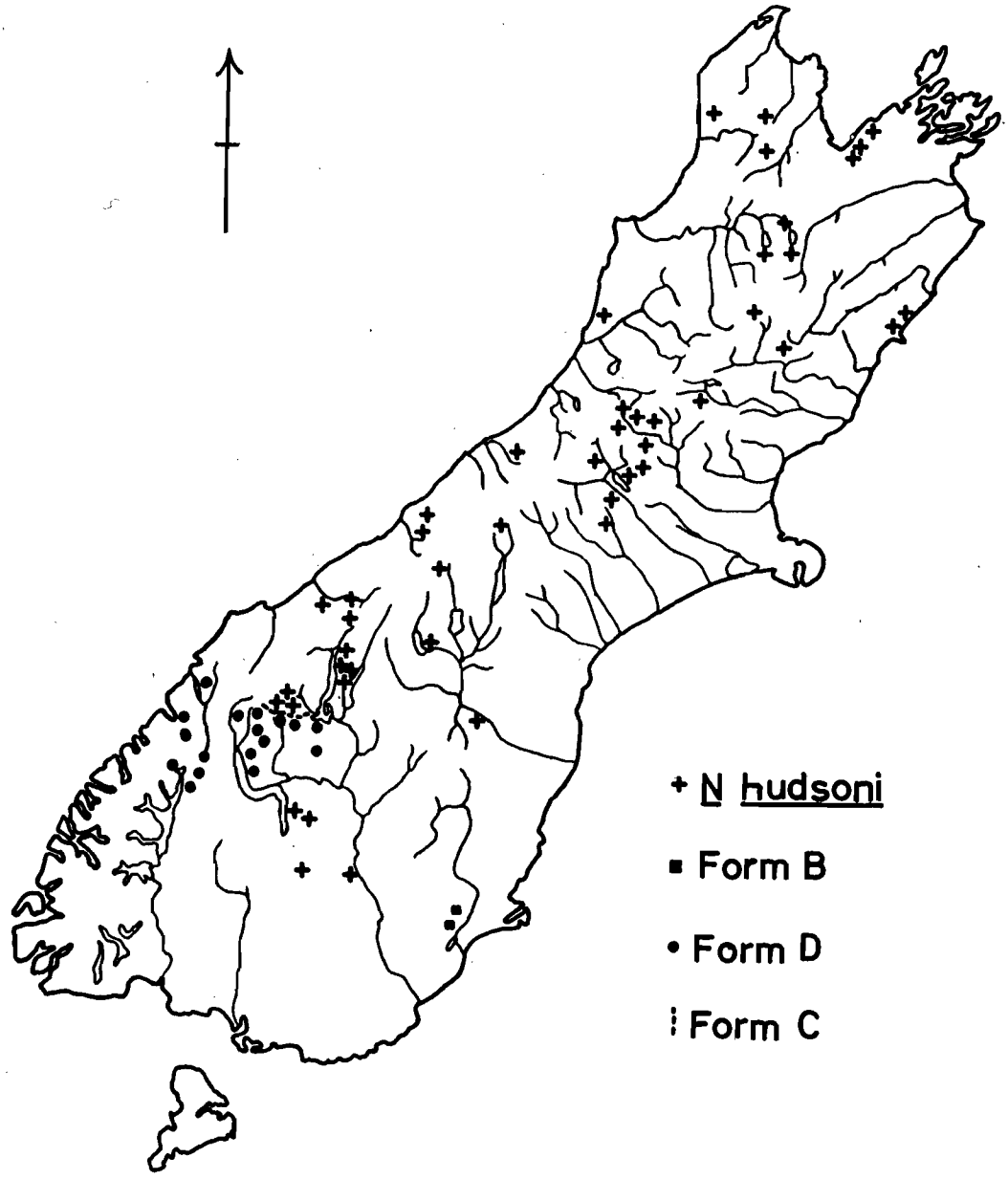

+ N hudsoni
■ Form B
• Form D
⁞ Form C

Figure 26. Map of South Island showing localities of *N. hudsoni* and Forms B, C and D.

than outer lamellae, lateral margins curved, constricted basally (Fig. 3).

Larva. Similar in all stages to N. hudsoni.

Locality Records.

Motatapu Gorge, Lake Wanaka, 1300 ft., P., D.A.C., 8-ii-66, Cant. Mus.;

Phoebe Creek, Matukituki Valley, Lake Wanaka, 1300 ft., P., D.A.C., 8-ii-66, Cant. Mus.;

Raspberry Hut, Matukituki Valley 1400 ft., P., D.A.C., 8-ii-66, Cant. Mus.;

Cadronna River, 3200 ft., L.P., D.A.C., 25-x-64, 11-i-65, Cant. Mus.;

12 Mile Creek, Queenstown, 1030 ft., L?, D.A.C., 25-x-64, (188);

Dooleys Creek, Queenstown, 1100 ft., L.P.A., D.A.C., 9-i-65, Cant.Mus.;

Ballarat Creek, Mount Aurum, L?, C.Devine, 23-iv-65, Cant. Mus.;

Invincible Creek, Rees Valley, 1500 ft., L?, D.A.C., 23-x-64, (182);

25 Mile Creek, Rees Valley 1550 ft., D.A.C., 23-x-64, (183);

Little Devil Creek, Rees Valley, 3150 ft., L?, D.A.C. 24-x-64, (184);

Lennox Falls, Rees Valley, 1550 ft., L?, D.A.C., 24-x-64, (186);

Eglington River, L?, V.M.S., 20-x-61, 223;

Walker Creek, Eglington River, L.P., V.M.S., 2-x-61, 225., D.A.C. & V.M.S., 17-i-64 (89a);

Worsley River, Lake Te Anau, A., Annon., 30-xii-27, Auck. Mus.;

Wesney Creek, Eglington River, 1200 ft., L.P.A., D.A.C. & V.M.S., 17-i-64, (90); annon., 31-i-65, Uni. Auck.;

45 Mile Creek, Eglington River, 1400 ft., L.P. D.A.C., & V.M.S., 17-i-64, (91);

Hollyford River, L.A., D.A.C. & V.M.S., 18-i-64, (93);

Jamestown River, Hollyford River, L?, S.C.Woods, ?-ix-64, Cant.Mus.;

Donne River, Milford Sound, 200 ft., L.A., D.A.C., & V.M.S., 19-i-64, (94);

Cleddau River, Milford Sound, 1050 ft., L?, D.A.C. & V.M.S., 19-i-64, (95);

Bowen Falls, Milford Sound, 50 ft., L?, D.A.C., 18-i-64, Cant.Mus.

Form D occurs in habitats similar to those occupied by N. hudsoni and appears to have a similar altitudinal distribution. The known area of distribution of Form D extends from Lake Wanaka to Milford Sound and Lake Te Anau (Fig. 26). No known collections of blepharocerids have been made in the area south of Lake Te Anau, but it is expected that Form D, and perhaps other blepharocerid forms, will eventually be discovered in that area.

Both sexes of Form D have very similar wings to the wings of N. hudsoni adults. The Form D females are very similar in head structure and genitalia to the females N. hudsoni. The Form D males have similar genitalia to the N. hudsoni males. However, the Form D males exhibit a dichoptic eye condition, which was first reported by Campbell (1923) and was apparently overlooked by Dumbleton (1963a).

Apart from the differences in the eye structure of the male and a slight difference in the shape of the pupal gill lamellae, Form D is very similar morphologically in all stages to N.hudsoni.

Classification of "Southern" Forms of Blepharocerid.

The classification of the southern forms will be considered from two aspects.

1. Classification based on Morphology.

Although Tonnoir (1923c) believed that larval characters were not taxonomically reliable, Van Emden (1957), Stuckenberg (1958) and Edwards (1929) consider larval characters to be of the same importance as adult characters in taxonomic work. These latter opinions are agreed with here and larval characters are used when considering classification.

Larvae: Dumbleton (1963a) described the colour of the 4th instar larva of N. hudsoni as "uniform dark brown", but does mention finding patterned N. hudsoni larvae. On this basis he suggested that the Dunedin and Queenstown larvae of Campbell (1921 and 1923. See below) be referred to N. hudsoni. Collections of N. hudsoni 4th instar larvae for this work show a range in colour, from a uniform colour to a pattern of colour (Plate 1a).

Though there is usually a range of colour in any larval population, patterned larvae are predominant in larval populations

sampled from regions in Nelson, West Coast and south of Mount Cook, while the uniformly coloured larvae predominate in larval populations from the region between Nelson and Mount Cook.

The "southern" larvae of Forms B & D, were first reported from Dunedin and Queenstown by Campbell (1921) who figured dorsal views of Queenstown larvae. He later (1923) figured more Queenstown larvae showing a range of colour patterning similar to that of the patterned N. hudsoni larvae.

As well as possessing similar colour patterns the larvae of N. hudsoni and Form D are morphologically indistinguishable.

Commensals: The commensal chironomid Dactylocladius commensalis often associated with N. hudsoni larvae, also occurs with Form D larvae. Tonnoir (1923b) believed the association to be specific, but D. commensalis does occur, though rarely, with larvae of N. campbelli. The significance of epizooic chironomids and their phylogenetic relationships ~~has~~ have been discussed by Steffan (1965), but this work was not available. However, it is considered here that it is unlikely for such an association between chironomid and blepharocerid to have arisen more than once within a single genus. The abundance of D. commensalis on both N. hudsoni and Form D is believed to be good evidence for conspecificity of these two blepharocerids. The rare occurrence of D. commensalis on N. campbelli larvae may indicate some relationship to the hudsoni-complex and is considered later (p.83).

Pupae: The pupae of Forms B & D are similar in all respects to N. hudsoni pupae except for a slight difference in shape and basal width length ratio of the outer lamella of the pupal gill. Pupal characters are not sufficiently distinct to provide positive identification of any New Zealand blepharocerid, so that the difference shown by "southern" pupae will not be considered further.

Adults: Campbell (1923) mentioned that the adults associated with the patterned Queenstown larvae showed wing venation similar to that of N. chiltoni and that the male eyes were dichoptic. However, the venation of Forms B and D is shown here (Figs. 5, 6 & 7) to be more similar to that of N. hudsoni than to that of N. chiltoni.

The differences in wing shape and venation between the New Zealand Neocurupira species are sufficient for the similarities in wing shape and venation of Forms C and D to indicate conspecificity with N. hudsoni. The wing shape of Form B (Fig. 6) is sufficiently different from the wing shape of N. hudsoni to make conspecificity doubtful.

Similarities in the shape of the dististyle and cercus of the male genitalia of Forms B, C & D are sufficient to indicate that these forms are conspecific with N. hudsoni. The apparent differences evident in Figure 19 of the genitalia of Form B are due to the drawing being made from a specimen dissected from a pupal case.

The oviscapts of the female genitalia of the hudsoni-group

all show the same basic pattern in the shape of the internal process which, when compared with oviscapts of the other Neocurupira species, could also indicate a close relationship between the "southern" forms and N. hudsoni (Figs. 11, 12 & 13).

The head structure of the female Form D (Fig. 17) is practically identical with that of the female N. hudsoni; however, the female head structure of Form B (Fig. 15) is considerably different and in the width of the vertex area, resembles N. campbelli females (Figs. 27 & 28).

The labial palpi of Forms B, C and D males (Figs. 10, 14 & 16) are shorter in relation to head depth, than those of N. hudsoni (Fig. 9). However, Form A, which is most probably N. hudsoni (p.21) also exhibits short labial palpi similar to Forms B, C & D, indicating that short labial palpi may not necessarily argue against conspecificity.

On the basis of the dichoptic eyed males, Forms C and D would previously have been placed in the subgenus Paracurupira, with the dichoptic but nearly holoptic eyed conditions of Form B making it difficult to place this form in either Paracurupira or Neocururpira. Because of this and other reasons discussed later (p. 36) the basis for the subgenus Paracurupira is shown to be unwarranted.

Even though the adults of Form C and D are fully dichoptic, the similarities of the larvae, male and female genitalia, wing shape and venation and shape of female head, to those of N. hudsoni, suggests that Forms C and D are morphologically conspecific with

N. hudsoni. Form B, though possessing morphologically similar larvae, similar male and female genitalia and similar venation to those of N. hudsoni, shows considerable differences in the structure of the female head and in the shape of the wing of both sexes and could be regarded as a subspecies.

2. Classification based on modern species concepts.

Mayr (1963) defines a species as " 'groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups' (Mayr 1940)". Hence as Form C is only known from populations that contain both N. hudsoni and Form D, and probably represents the hybrid of these two blepharocerids, by Mayr's definition, Form D and N. hudsoni must be conspecific. The geographically isolated Form B may perhaps represent a subspecies. This conclusion is the same as that arrived at on purely morphological grounds. Bigelow (1965), however, shows that hybridization does not necessarily mean conspecificity if the hybrid zone has been maintained for long periods of time, for this indicates a restricted gene flow. If the gene flow was unrestricted, the hybrid zone would not be evident and perhaps a cline of variation or a homogenous population would result. Bigelow maintains that the presence of the two parent forms in the hybrid zone indicates a highly restricted gene flow and that the two parents are still to be considered as species, since the gene flow will never result in conspecificity.

The situation where the two parent forms are present in the hybrid zone appears to be applicable to N. hudsoni and Form D in the Matukituki Valley, Lake Wanaka, for both these parent forms as well as the apparent hybrid Form C are found in the same populations.

Unfortunately the amount of material available from this locality is extremely meagre and it would be dangerous to draw definite conclusion about the reproductive isolation of Form D and N. hudsoni. It is because of this lack of material concerning the reproductive isolation of the hudsoni-complex, that the blepharocerid forms found south of the area of distribution of N. hudsoni, are given the arbitary lettering used here and are not given any taxonomic rank.

The final taxonomic status of Forms B, C & D will require a detailed examination of the situation occurring at the junctions of the areas of distribution of these forms with that of N.hudsoni.

The Validity of the subgenus Paracurupira.

Even though the relationships within the hudsoni-complex cannot at present be determined, it is obvious that the blepharocerids that constitute this complex are morphologically very closely related, not only in the larval stages but in most of the adult characters as well. As mentioned previously (p.34) the present classification of New Zealand Neocurupira would place constituents of the hudsoni-complex into separate subgenera. The variation

in male eye structure within the hudsoni-complex, from holoptic N. hudsoni through intermediate Form B to dichoptic Forms C and D, is comparable to the intrageneric eye variation in the South African Elporia (Stuckenberg 1955).

Because dichoptic and holoptic eyed Neocurupira males show very close relationship (perhaps even conspecific) within the hudsoni-complex, the separation of Neocurupira into the subgenera Neocurupira and Paracurupira on the basis of holoptic eyed males in Neocurupira and dichoptic eyed males in Paracurupira is considered to be unwarranted and Paracurupira is passed into synonymy.

Neocurupira (N) campbelli Dumbleton

Neocurupira (Paracurupira) campbelli Dumbleton, 1963, N.Z. J. Sci., 6, 2: 234-258.

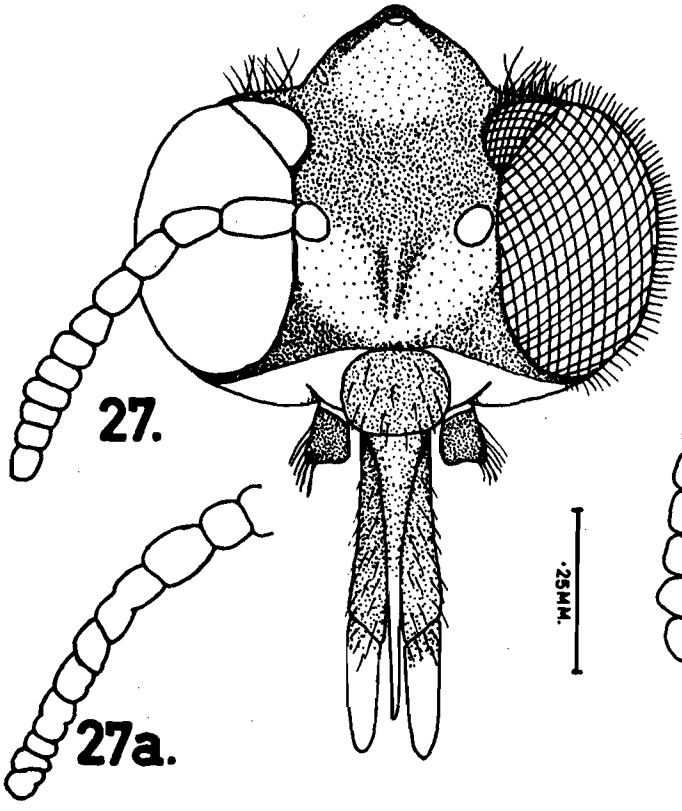
Adult.

Male. Body length 4.5-6.8 mm.

Head.

Head depth width ratio 1:1.2; eye ratio 1:2; vertex width 0.28 of head width; Antennae 11-segmented; labrum shorter than labial palpi; labial palpi subequal in length to head depth.

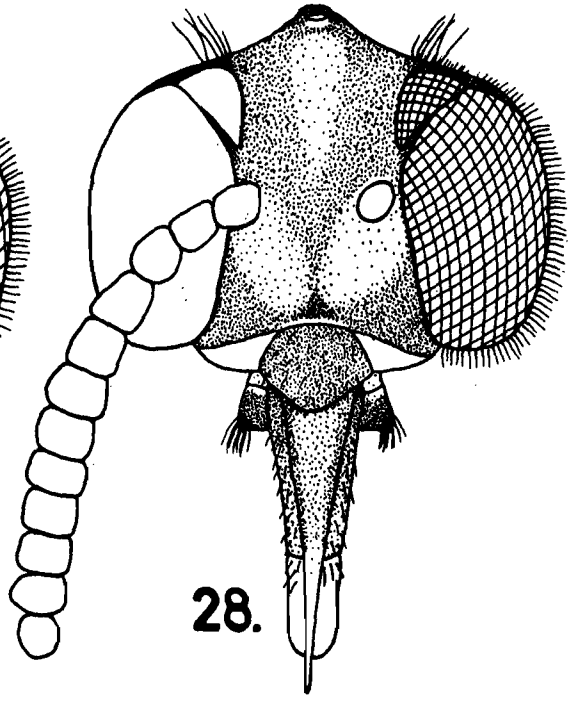
Genitalia (Fig. 36). Posterior margin of cercus broadly concave, lateral margins rounded.



27.

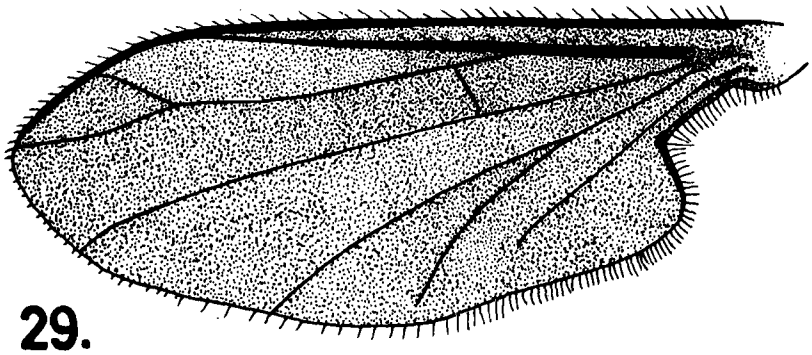
27a.

·25MM.



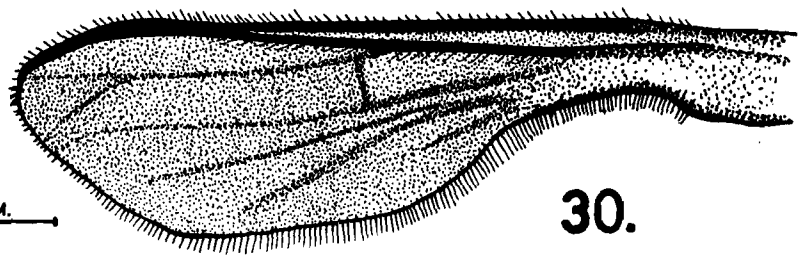
28.

1MM.



29.

·5MM.



30.

Figures:-

27. Frontal view of head of macropterous N. campbelli female.

27a. Aberrant antenna of macropterous N. campbelli female.

28. Frontal view of head of brachypterous N. campbelli female.

29. Macropterous wing of N. campbelli female.

30. Brachypterous wing of N. campbelli female.

Female. (Macropterous). Body length 5.6-9.0 mm; wing length 3.5-4.0 mm.

Head (Fig. 27). Head depth width ratio 1:1.4; eye ratio 1:4.2; vertex width 0.31 times as wide as head-width; antennae 12-segmented; clypeus rounded; labrum shorter than labial palpi; labial palpi sub-equal in length to head depth, first labial palpi segment shorter than labrum.

Genitalia (Fig. 35). Internal process of oviscapt conical, oviscapt lobes bearing 7-9 clear short spines subapically.

Female. (Brachypterous). Body length 5.0-6.0 mm. Wing length 0.6-2.5 mm.

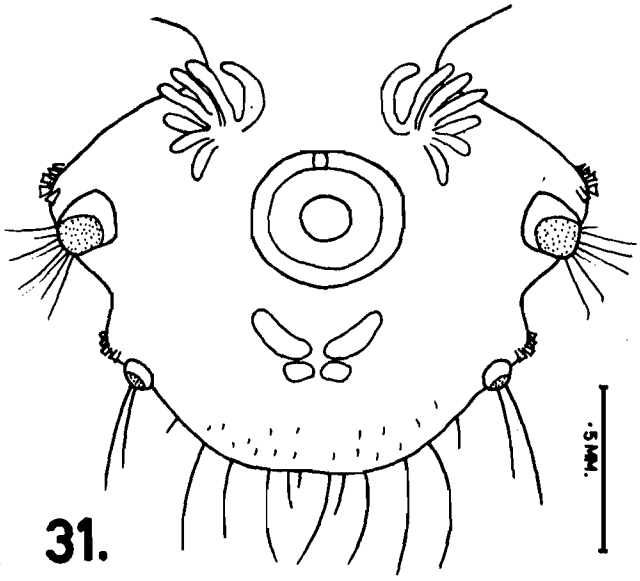
Head (Fig. 28). Head depth width ratio 1:1.2; eye ratio 1:3.5; vertex width 0.28 times as wide as head-width; antennae 12-segmented; clypeus subangulate laterally and distally; labial palpi variable in length.

Genitalia (Fig. 34). Internal process of oviscapt concave apically, oviscapt lobes bearing 7-9 black short spines sub-apically.

Pupa. Length 4.0-6.2 mm. Outer lamellae of pupal gills tapering to narrow rounded apex; basal width length ratio of outer lamellae 1:3.4.

Larvae.

Fourth Instar. (Fig. 31). Length 4.4-8.0 mm. Sucker width 0.48-0.59 mm. Colour uniform dusky yellowish brown (10YR2/2), abdominal



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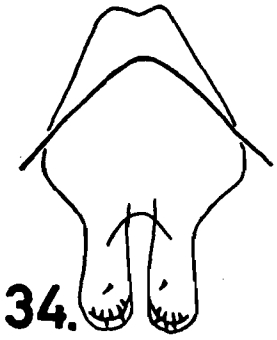

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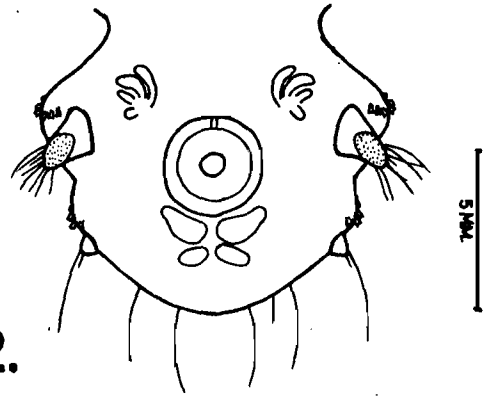

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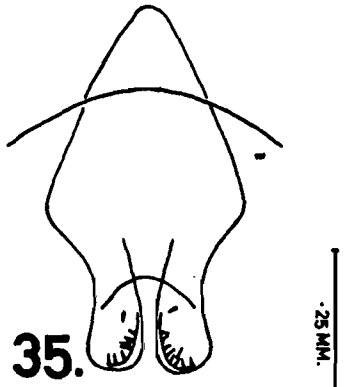

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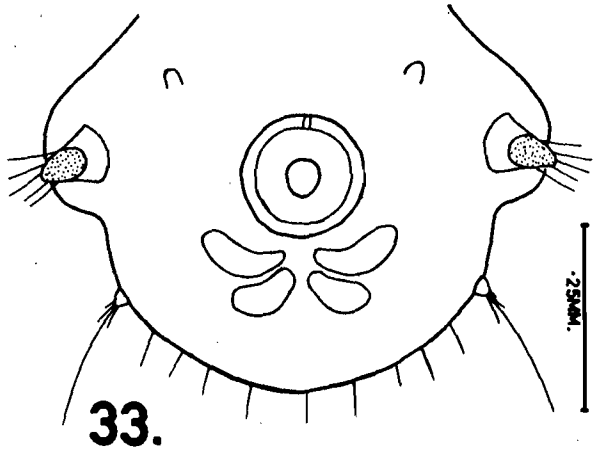

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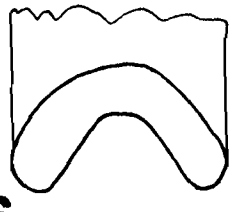


36.

prolegs rounded apically, not angulate laterally; posterior margin of anal division bearing 6-12 irregularly arranged black hairs.

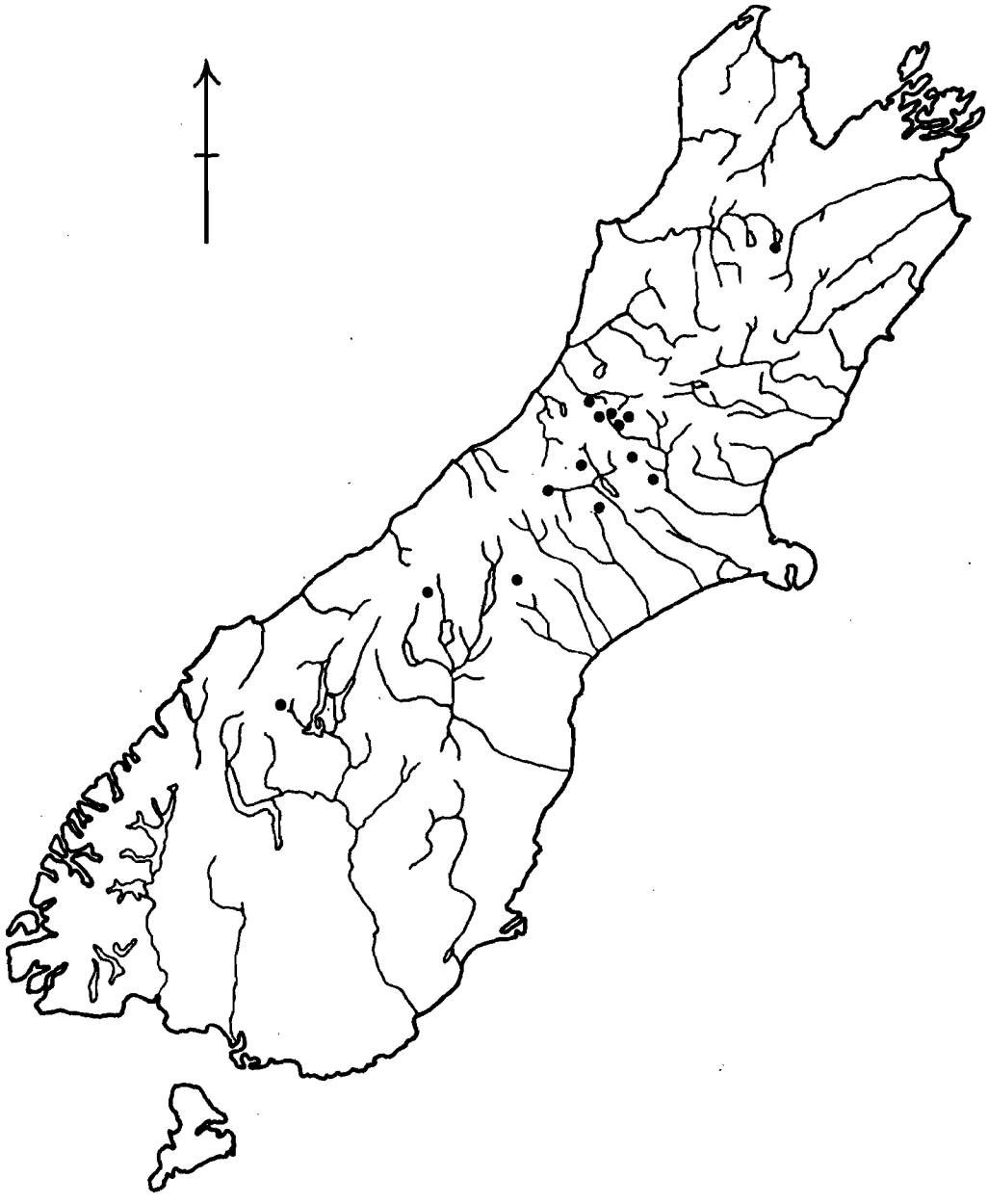
A small sample of larvae similar to the fourth instar larvae of N. campbelli was collected from the Matukituki Valley, Lake Wanaka, (26-x-64) in association with N. hudsoni larvae. These larvae were jet black instead of the normal dusky yellowish brown, even the normally clear cone-shaped scales of the dorsal marginal armature being black. The sucker width was larger 0.59-0.68 mm. A single pharate male adult of N. campbelli has since (8-ii-66) been found from the same location. (Unfortunately the sample of larvae has been misplaced.)

Third instar. (Fig. 32). Length 2.8-4.7 mm. Sucker width 0.30-0.36 mm. Colour of cephalic sclerites black; remainder of body uniformly dark brown (5YR2/4) to brownish black (5YR2/1); cephalic sclerites occupying 1/3 (early) to 1/2 (late) of length of cephalic division; marginal armature of setae; no apparent dorsal armature; lateral margins of median divisions rounded; abdominal prolegs slightly longer than basal width, cone shaped, sharply rounded apically, bearing dorsally 10-12 fine hairs as long as ventral pad; ventral pad occupies $\frac{1}{3}$-$\frac{1}{2}$ of length of proleg; seventh proleg as long as wide, bearing apically two black hairs, one 5 times as long as proleg; anal division separated laterally from fifth median division by very shallow angulate constriction; posterior margin of anal division

broadly rounded bearing 4-5 black hairs irregular ly arranged, as long as seventh proleg hairs; eight tracheal gill filaments per division.

One third instar larva was available from the Matukituki Valley collection. Colour, jet black; sucker width 0.40-0.45 mm.

Second Instar. (Fig. 33). Length 1.9-2.6 mm. Sucker width 0.17-0.18 mm. Colour of cephalic sclerites black; remainder of body uniformly dark brown (5YR2/4); cephalic sclerites occupying 1/3 (early) to 1/2 (late) length of cephalic division; no marginal armature, dorsal armature consisting of lanceolate setae, pattern similar to spines on 3rd instar of N. chiltoni; dorsal cuticle microsculptured into grooves and ridges; lateral margin of median divisions same as for 3rd instar; abdominal prolegs as long as basal width, cone shaped, sharply rounded apically, bears dorsally fine pale hairs as long as pad, ventral pad occupies 1/2 of proleg length; seventh proleg small, as long as basal width, bearing apically one black hair 5-7 times as long proleg, plus 2-3 shorter hairs; anal division not separated laterally from fifth median division by constriction; posterior margin anal division broadly rounded and continuing beyond the 7th proleg to the fifth division, bearing 7-9 short black hairs; two small tracheal gills per division.



Locality Record.

Hakano Stream, Travers River, Lake Rotoiti, Nelson, 3500 ft., L., J. Flux, 25-xi-64, Cant. Mus.;

Townsend Creek, Minchin Pass, Arthur's Pass, S59. 282485., 3800 ft., L.P., D.A.C., 18-iv-65, Cant. Mus.;

Linwood Creek, Minchin River, S59. 278455., 2500 ft., L.P.A., D.A.C., 18-iv-65, Cant. Mus.;

Temple Basin, Arthur's Pass, S59. 067324., 4375 ft., L., D.A.C., 20-xi-63; 4500 ft., D.A.C., 22-xi-64, Cant. Mus.;

Lower Otira River Gorge, L.P., V.M.S., 12-iii-65, Cant. Mus.;

Pegleg Creek, Arthur's Pass, S59. 055340., L.P.A., L.J.D., 13-iv-62, Ent. Div. L.; D.A.C., 15-xii-62, Cant. Mus.;

Bealey Chasm, Arthur's Pass, S59. 050313., 2700 ft., L.P.A., D.A.C., 1962-1966, Zoology Department, University of Canterbury;

Bealey River, S59. 054296., 2400 ft., L., D.A.C., 7-ii-62, Cant.Mus.;

McGrath's Creek, Arthur's Pass, S59. 053300., 2600 ft., L., D.A.C., 29-vii-62, Cant. Mus.;

Punch Bowl, Arthur's Pass, S59. 055295., 2400 ft., L.P.A., D.A.C., 20-i-62, 20-i-63, Cant. Mus.;

Avalanche Creek, Arthur's Pass, S59. 054285., 2600 ft., L., D.A.C., 4-i-62, Cant. Mus.;

Rough Creek, Arthur's Pass, S59. 045275., 2500 ft., L. P., D.A.C., 16-xii-62, Cant. Mus.;

Snow Creek, Arthur's Pass, S59. 065264., 2000 ft., L.P., D.A.C., 28-ix-63, Cant. Mus.;

Halpin's Creek, Arthur's Pass, S59. 070244., A., L.J.D., 13-iv-62, Ent. Div. L.;

Mingha River, S59. 114297., 2000 ft., L.P., D.A.C. 16-xii-63, Cant. Mus.;

Masons Stream, Flock Hill, Craigieburn Mountain Range, 3800 ft., A., P.M.Johns, 21-i-65, Cant. Mus.;

Linden Stream, Fog Peak, Porter's Pass, S74. 218864., 3500 ft., L.P., R.S.Bigelow, 13-ii-26; A.G.McFarlane, 25-xi-64, Cant. Mus.;

Mount Hutt, 2500 ft., L.P.A., G. Tunnicliffe & W.P.Thomas, 29-i-64, Cant. Mus.;

Kakapo River, Wilberforce River, 2000-3800 ft., L.P., D.A.C., 18-x-63, Cant. Mus;

Kiwi River, Wilberforce River, 2100 ft., L., D.A.C., 19-x-63, Cant. Mus.;

Lyell Glacier, Rakaia River, A., P.M.Johns, 25-xi-64, Cant. Mus.;

Fox Peak, Two Thumb Mountain Range, 3000 ft., 4500 ft., D.A.C., 20-x-63, (6), (7), (9);

Black Birch Stream, Mount Cook, 2500 ft., 2750 ft., L.P., D.A.C. & V.M.S., 9-i-64, (59 & 59c);

Old Homestead Creek, Matukituki River, Lake Wanaka, 1400 ft., L.P., D.A.C., 26-x-64, (190); 8-ii-66, Cant. Mus.;

Dumbleton (1963a) considered that N. campbelli was of restricted distribution occuring only in the Arthur's Pass region. However, since then collections show the area of distribution to extend from Lake Rotoiti, Nelson, to Lake Wanaka, Otago (Fig. 37). N. campbelli occurs, with N. hudsoni when the areas of distribution coincide and in similar habitats. The altitudinal distribution is from 1400 ft. to 4500 ft. above sea level.

Dumbleton (1963a) did not possess any evidence to show seasonal variation in the proportions of the brachypterous females in a population. It has been shown (Chpt. III) that there is a significant negative linear regression of % female pupae that are brachypterous on mean water temperature, and that the collections of N. campbelli female adults show a seasonal pattern, with macropterous females occuring from December - March and the brachypterous females from March - May.

The female macropterous wing and the male wing are very similar (Fig. 29). The female brachypterous wing (Fig. 30) varies in length from 0.6-2.5 mm. The longest wing could possibly be used for flight but in all cases, dissection showed that the flight muscles were atrophied. The trichiation and development of the veins C and R_1 are similar in the macropterous and brachypterous wings, but the veins R2+3, R4+5, M1, M4, Cu1 and A1 of the brachypterous wing are poorly developed (Fig. 30).

The head depth width ratio of the macropterous female is greater than that of the brachypterous female; the ocellar turret

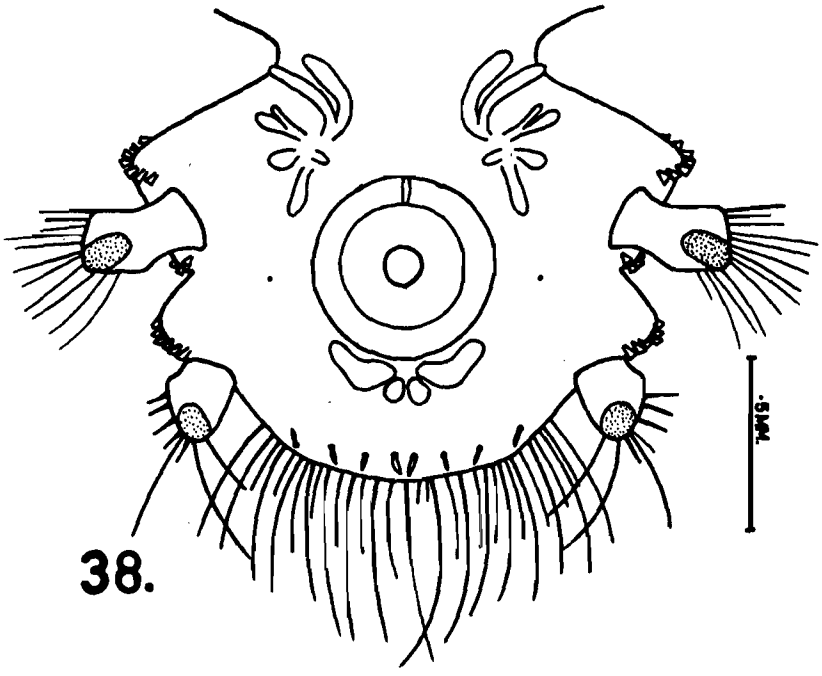
is rounder, protrudes further and the clypeus is more rounded than those of the brachypterous winged female. The labial palpi of the brachypterous female are variable, ranging from just longer than the labrum to shorter than the labrum (Fig. 28). The antennal segments of both forms of female are normally distinct, but there are occasional adults with the antennal segments partially or completely fused in an irregular manner (Fig. 27a).

Craig (1963) (Appendix I) first reported the occurrence of the Nematode Agamomermis sp. in N. campbelli adults and pupae. Parasitised males exhibit the female number of 12-antennal segments, and it is possible that the nematodes castrate the males though no dissection has been carried out to show whether in fact this does happen. Parasitised females show no apparent external morphological effects.

Similar effects are produced by Agamomermis sp. parasitising the males of Culicoides (Ceratopogonidae) (Callot 1959). The effect of nematodes on other groups of insects is well documented (e.g. Imms 1957).

Neocurupira (N) chiltoni (Campbell).

? Curupira Chilton, 1905, Trans. N.Z. Inst., 38; 277-278.
Curupira chiltoni Campbell, 1921, Trans. N.Z. Inst., 53; 260-262.
Paracurupira chiltoni, Campbell, 1923, Trans. N.Z. Inst. 54; 260-264.
Neocurupira (Paracurupira) chiltoni, Alexander, 1958, Proc. 10th Int. Congr. Ent. (1956), 1, 824; Dumbleton, N.Z. Jour.Sci. 6, 2; 234-258.



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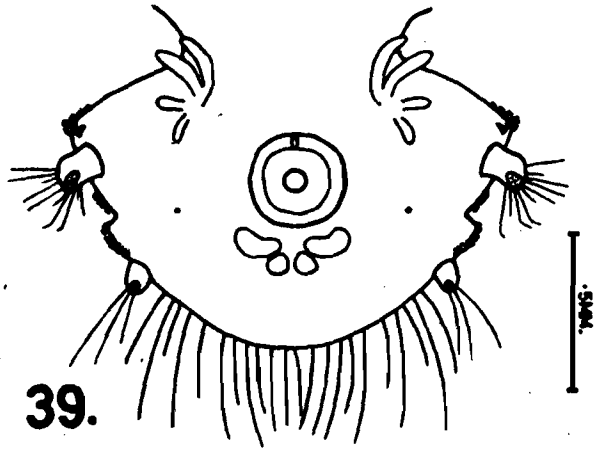

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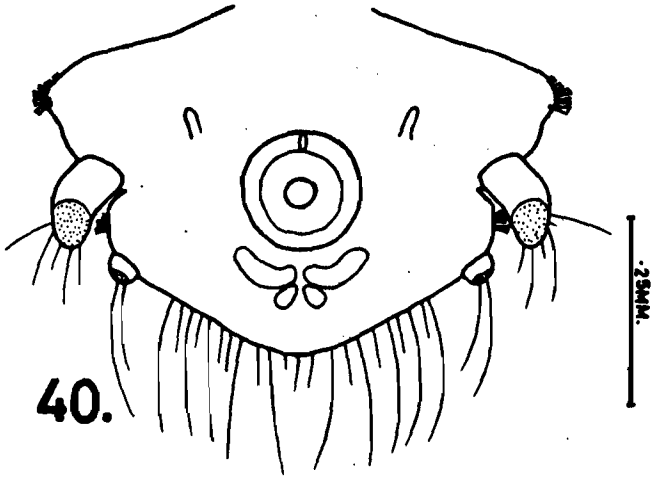

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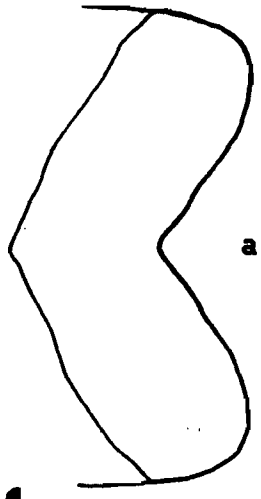

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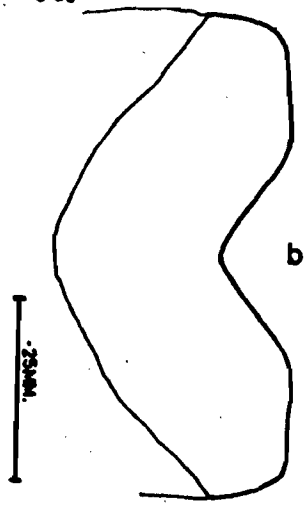
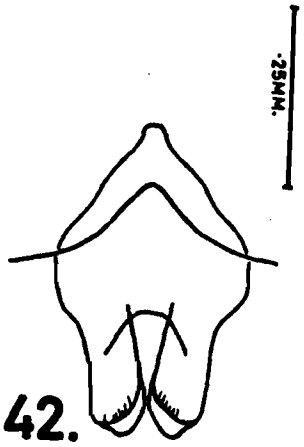




42.

Adult.

Male. Head. Head depth width ratio 1:1.2; Eye ratio 1:1; vertex 0.12 times as wide as head width; labial palpi twice as long as head depth.

Genitalia. (Fig. 41a & b). Cercus wide, shallowly concave medianly, rounded laterally, variable.

Female. Head. Head depth width ratio 1:1.4; Eye ratio 1.0:2.0; vertex 0.2 times as long as head depth; labial palpi less than twice as long as head depth.

Genitalia (Fig. 42). Internal processof oviscapt constricted subapically, rounded apically; oviscapt lobes bearing 7-9 fine clear spines subapically.

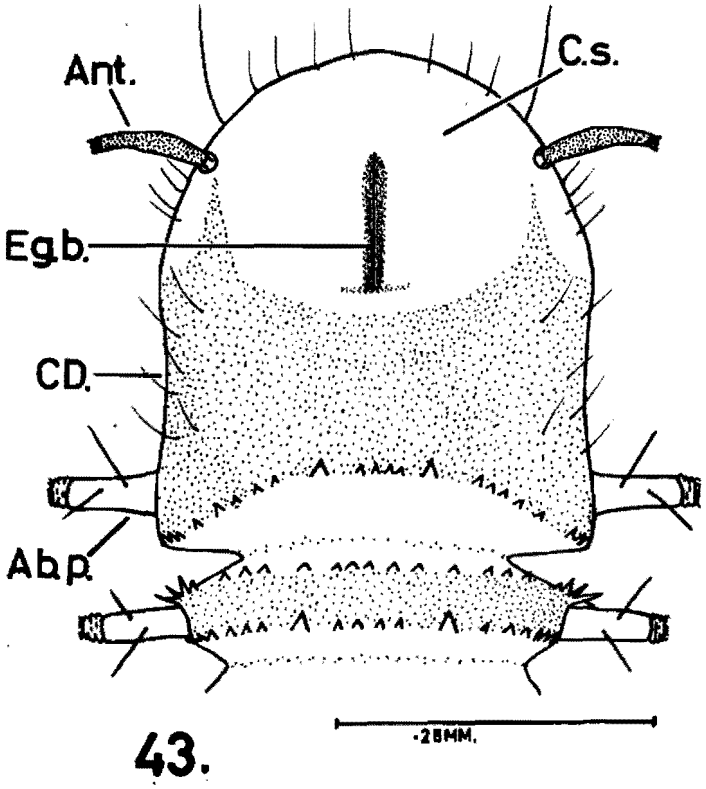
Pupa. Length 4.1-8.2 mm. Outer lamellae of pupal gills long, almost parallel-sided, rounded apically, basal width length ratio of outer lamellae 1:3.6.

Larvae.

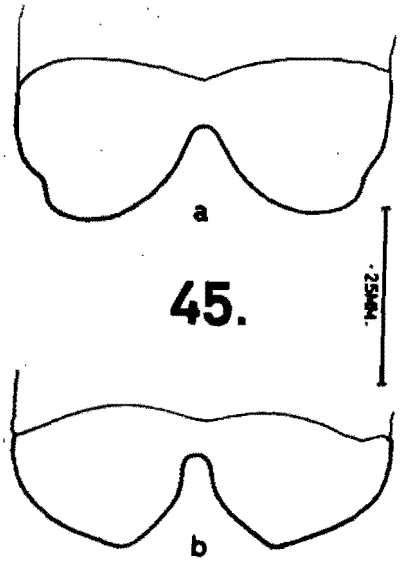
Fourth Instar (Fig. 38). Length 5.1-10.5 mm. Sucker width 0.60-0.65 mm. Colour. Normally uniform, varying from dusky brown (5YR2/2) (early), to moderate brown (5YR4/4), or light brown (5YR5/6) (late), occasionally exhibiting patterning of third instar larvae; dorsal armature consisting of large black spines; abdominal prolegs pointed apically, angulate laterally, constricted basally

Third Instar. (Fig. 39). Length 2.6-5.6 mm. Sucker width 0.30-0.36 mm. Colour cephalic sclerites dark brown (5YR2/4); remainder of body normally uniform moderate brown (5YR3.5/4) but often with dorsal triangular greyish-orange (10YR7/4) patch on 4th median division and lighter patches of colour lateral to the cephalic sclerites; cephalic sclerites occupy3/10 (early) to 3/5 (late) length of cephalic division; marginal armature of scales; dorsal armature of raised tubicles bearing short, thick spines in the same pattern as large dorsal spines of 4th instar, as well as smaller setae with irregular arrangement; lateral margins of median divisions angulate anteriolaterally rounded posteriolaterally, straight between; abdominal prolegs slightly less than twice as long as basal width, constricted subbasally, angulate apically and laterally, dorsally bearing five longer hairs, as long as ventral pad, plus other finer hairs, ventral pad 1/3 as long as proleg; seventh proleg slightly indented into posterior margin, longer than basal width, bearing three black hairs three times as long as the proleg; anal division separated laterally from fifth median division by a constriction sharply angulate posteriorly, sloping gently anteriorly; posterior margin of anal division broadly rounded bearing 18-22 black hairs slightly longer than seventh proleg hairs; eight tracheal gills per division; posterior filaments of anal gills 1/3 size of anterior filaments.

Second instar (Fig. 40). Length 2.0-2.9 mm. Sucker width 0.18-0.19 mm. Colour of cephalic sclerite darker than that of remainder of



43.



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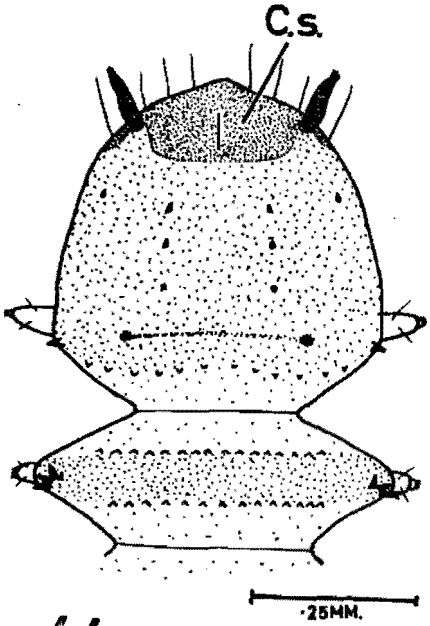

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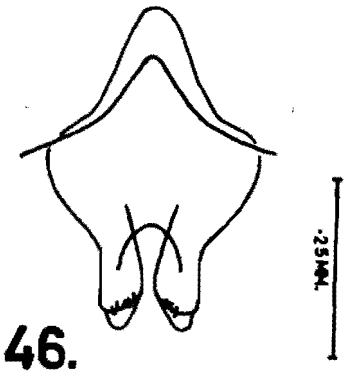


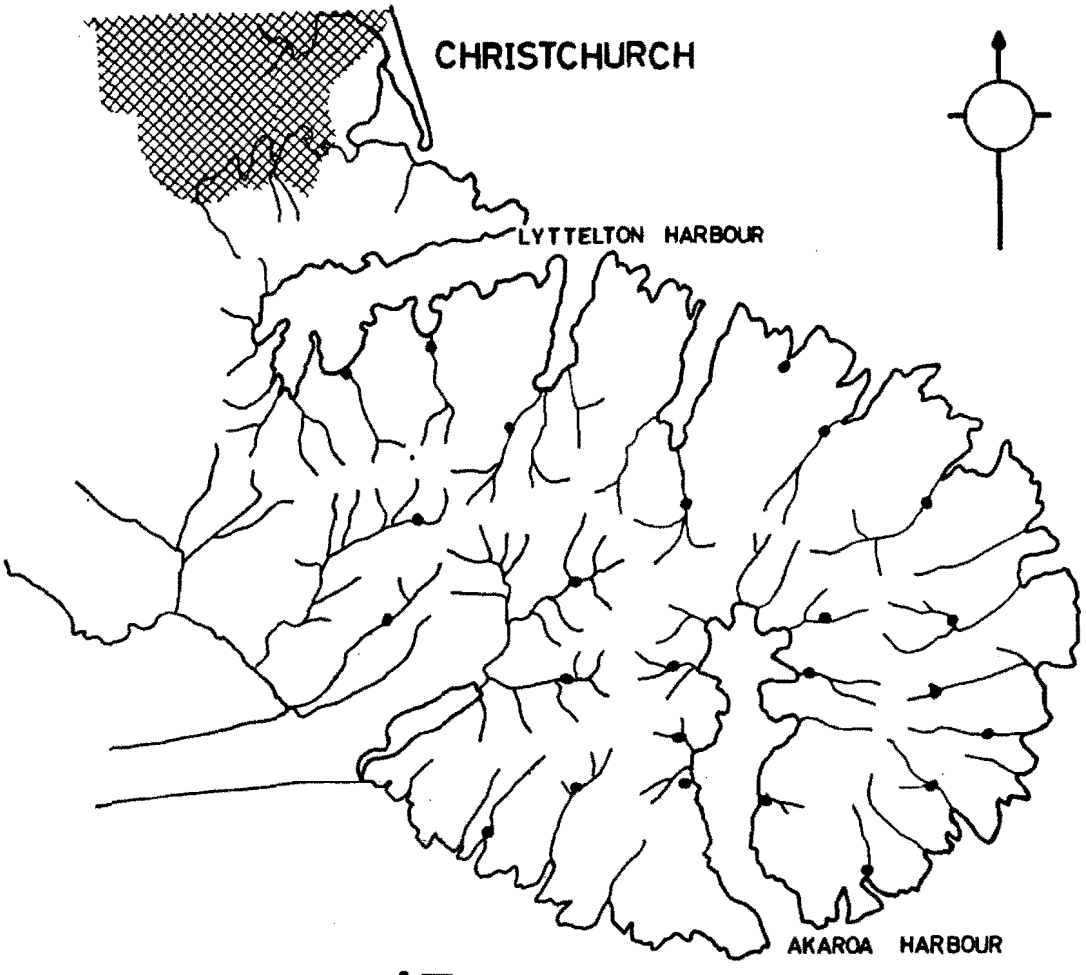
46.

body; remainder of body varying from moderate brown (5YR3/4) (early) to moderate yellow brown (10YR5/4) (late); cephalic sclerites occupy ½ (early) to ⅓ (late) length of cephalic division; ocelli show as reddish structures postero-lateral to cephalic sclerites; marginal armature of scales; dorsal armature of small raised tubicles in same pattern as 3rd instar; dorsal cuticle micro-sculptured into grooves and ridges; lateral margins of median divisions angulate, terminal areas straight; abdominal prolegs twice as long as basal width, rounded apically, slightly constricted laterally; dorsally bearing 2-3 brown hairs as long as ventral pad as well as other finer hairs; ventral pad occupying 1/3 of the proleg length; seventh proleg as long as basal width, bearing two black hairs three times as long as proleg; anal division separated laterally from fifth median division by deep acutely angulate constriction; posterior margin of anal division very broadly subangulate, bearing 6-10 hairs four times as long as the seventh proleg, plus 12-14 shorter hairs; two tracheal gill filaments per division; posterior filaments of anal gills 1/3 size of anterior filaments.

First Instar. (Figs. 43 & 44).

(Hatched in laboratory from eggs laid by N. chiltoni females).

Length 0.8-1.6 mm. Sucker width 0.057-0.067 mm. Colour uniform, light brownish grey (5YR6/1) (early), to light brown (5YR6/4) (late); cephalic sclerites of body colour occupy 1/2 (early) to 1/4 (late) length of cephalic region ; antennae one-segmented, bearing sensory



47.

spines distally; no marginal armature; dorsal armature as rows of stout black spines across anterior and posterior surfaces of divisions, larger spines on lateral edge of divisions; lateral margins of median divisions acutely angulate anteriolaterally, obtusely angulate posteriolaterally (early Fig. 44); acutely rounded apically (late Fig. 43); abdominal prolegs conical with extensile tip, bearing dorsally two black hairs; seventh proleg small conical structure bearing single black hair; anal division separated laterally from fifth median division by subangulate constriction; posterior margin of anal division bare, highly rounded; no tracheal gills.

Locality Records.

Banks Peninsula.

Charteris Bay, S84. 060412., 5 ft., D.A.C., 5-vii-65, Cant. Mus.;

Purau Valley, Annon, 23-xi-19, Dom. Mus. & Auck. Mus.; J.W.Campbell, 6-i-21, Ent. Div. N.; A.L.Tonnoir, 2-ii-22, Cant. Mus.; L.J.D. 22-x-59, 9-ii-62, Ent. Div. L.; S84. 105409., D.A.C., 1962-1966, Zoology Department, University of Canterbury & Cant. Mus.;

Port Levy, S84. 139365., 500 ft., D.A.C., 14-xii-65, (211);

Kukupa, S84. 233330., 300 ft., D.A.C., 14-xii-65, (212);

Little Akaloa, S84. 296365., 300 ft., D.A.C., 14-xii-65, (213);

Menzies Bay, P.M.Johns, ?-xiii-55, Cant. Mus.;

Okains Bay, S85 & S95. 329351., 320 ft., D.A.C., 14-xii-65, (214);

Le Bons Bay, S85. & S95. 374275., 150 ft., D.A.C., 15-xii-65, (215);

Hickory Bay, S85 & S95. 356238., 1100 ft., D.A.C., 15-xii-65, (216);

Goughs Bay, S85 & S95. 373224., 300 ft., D.A.C., 15-xii-65, (217);
Otanerito (Long) Bay, S85 & S95. 358195., 200 ft., D.A.C., 15-xii-65, (218);
Flea Bay, S94. 326153., 10 ft., D.A.C., 15-xii-65, (219);
Akaroa, C. Chilton, ?-ii-03, Ent. Div. N.;
Onuku, Akaroa, S94. 272188., 5 ft., D.A.C., 13-xii-65, (208);
Takamatua Bay, S94. 298252., 50 ft., D.A.C., 13-xii-65, (209);
Robinsons Bay, S94. 304280., 200 ft., D.A.C., 13-xii-65, (210);
French Farm Bay, S94. 228258., 150 ft., D.A.C., 13-xii-65, (207);
Wainui Bay, S94. 225222., 100 ft., D.A.C., 12-xii-65, (205);
Cape Three Points, S94. 236197., 10 ft., C.S.Woods, 16-viii-64, Cant. Mus.;
Peraki Bay, S94. 175188., 350 ft., D.A.C., 11-xii-65, (203);
Te Oka Bay, S94. 133184., 10 ft., D.A.C., 12-xii-65, (206);
Okuti Valley, S94. 176251., 150 ft., D.A.C., 12-xii-65, (204);
Opuahau Stream, Little River, S94, 176299., 200 ft., D.A.C., 16-xii-65, (220);
Little River, L.J.D., Ent. Div. L;
Prices Valley, S94. 075279., 200 ft., D.A.C., 16-xii-65., (221);
Kaituna, S. Lindsay, 16-iii-29, Cant. Mus., D.A.C., 1963-1966, Zoology Department, University of Canterbury.

N. chiltoni is found only on Banks Peninsula, Canterbury (Fig. 47). A report by Campbell (1923) that this species was found at Arthur's Pass is evidently an error, for no subsequent reports have

been made despite intensive collecting in that area. It is possible that Campbell mistook the larvae of N. tonnoiri for those of N. chiltoni as the early larval instars are very similar.

N. chiltoni is widely distributed on Banks Peninsula, particularly on the western slopes, occurring in practically every valley that possesses a stream with a water flow sufficient to keep some rocks clear of heavy algal growths. It occurs at altitudes from just above sea level to 1100ft.

The fourth instar of N. chiltoni is unusual in that it is the only New Zealand species of blepharocerid to possess strong black dorsal spines.

Neocurupira (N) tonnoiri Dumbleton

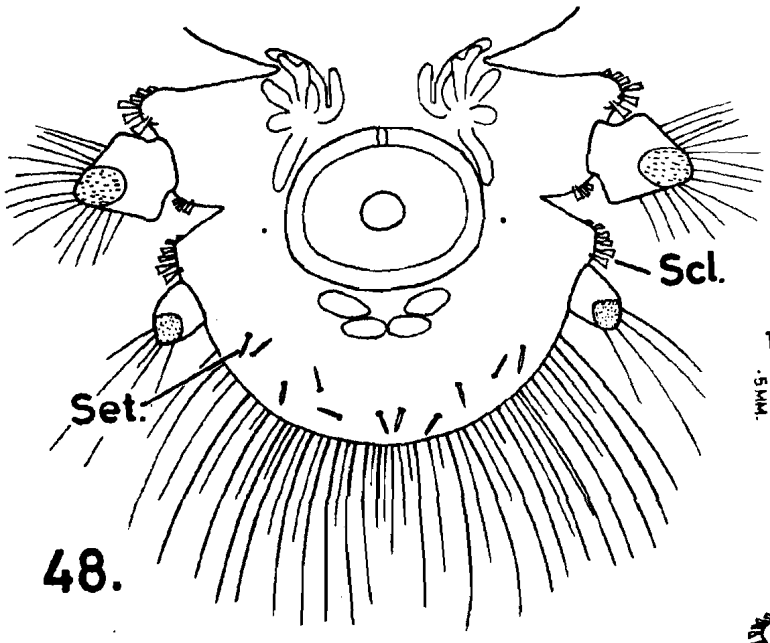
Neocurupira (Parcurupira) tonnoiri Dumbleton, 1963, N.Z. J. Sci., 6, 2: 234-258.

Adult.

Male. Head. Head depth width ratio 1:1.3; eye ratio 1:2.1; vertex 0.25 times as wide as head width; antennae 15-segmented; labial palpi twice as long as head depth,

Wing (Fig. 51). Anal angle of wing approximately 110°, veins reaching wing margin.

Genitalia (Fig. 45). Cercus variable, deeply recorded median concavity.



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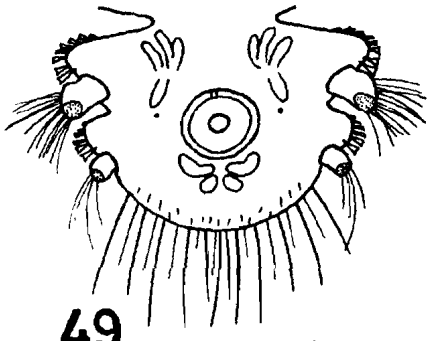

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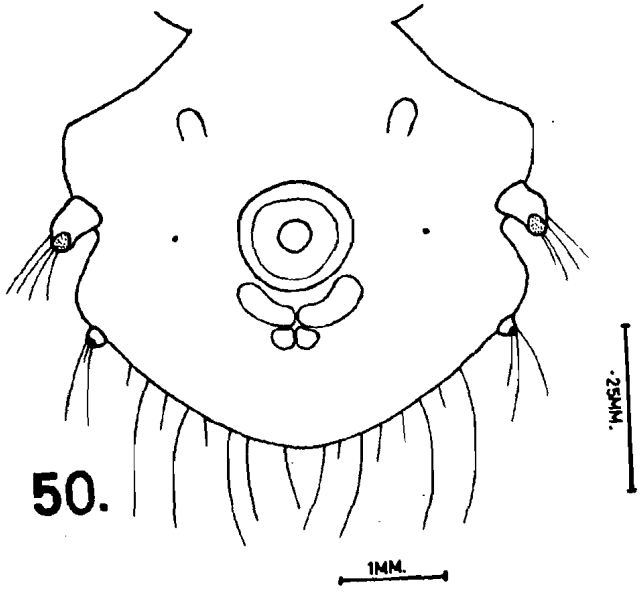

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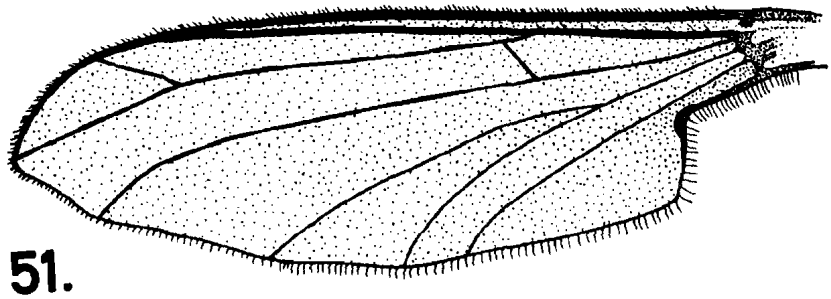


51.

Figures:-

48. Ventral view of posterior end of N. tonnoiri fourth instar larva.

49. Ventral view of posterior end of N. tonnoiri third instar larva.

50. Ventral view of posterior end of N. tonnoiri second instar larva.

51. Wing of N. tonnoiri male.

Abbreviations:-

Set. - Setae.

Scl. - Scales.

Female. Head. Head depth width ratio 1:1.4; eye ratio 1:2.3; vertex .33 head width; labial palpi twice as long as head depth; second labial palpi segment as long as labrum. Genitalia (Fig. 46). Internal process of oviscapt conical apically; oviscapt lobes bearing 4-6 short black spines subapically.

Pupae. Length 5.0-5.5 mm; outer pupal gill lamellae tapering with apex narrow but rounded, basal width length ratio 1:3.4.

Larvae.

Fourth instar (Fig. 48). Length 4.5-8.6 mm. Sucker width 0.54-0.64 mm. Colour of cephalic sclerites moderate brown (5YR3/4) peripherally, yellowish orange (10YR7/6) medially; remainder of body patterned, variable, from background of dark brown (5YR2/4) with patterning of yellowish orange (10YR7/6), to background of dusky yellowish brown (10YR2/2) with patterning dark yellowish orange (10YR6/6) (Plate 1b); dorsal armature of small flattened spines; abdominal prolegs pointed apically, angulate laterally, constricted basally.

Third instar (Fig. 49). Length 3.3-4.7 mm. Sucker width 0.26-0.32 mm. Cephalic sclerites black; remainder of body varying from uniform moderate brown (5YR4/4) to moderate brown with yellowish (5Y7/4) lateral lunar markings; from 1/3 (early) to 1/2 (late) length of cephalic division occupied by cephalic sclerites; marginal armature of scales; dorsal armature of irregularly arranged setae; dorsal cuticle microsculptured

into fine grooves and ridges; lateral margins of median divisions sub angulate anteriolaterally, terminal margins straight, rounded posteriolaterally; abdominal prolegs slightly longer than basal width, pointed apically, constricted sub basally, bearing dorsally 15-20 clear yellowish hairs slightly shorter than the proleg, ventral pad occupying 1/3 length of proleg; seventh proleg relatively large, slightly longer than basal width, bearing apically 3-5 hairs, two to three times as long as proleg; anal division separated laterally from fifth median division by deep acutely angulate constriction; posterior margin of anal division rounded with seventh proleg indented, bearing 10-14 clear hairs as long as seventh proleg and hair, shorter hairs alternating with longer hairs, row of 17-19 short setae ventral and parallel to the posterior margin; 8 tracheal gill filaments per division.

Second Instar (Fig. 50). Length 2.0-2.8 mm. Sucker width 0.14-0.18 mm. Cephalic sclerites dark brown (5YR2/4); remainder of body varying from uniform moderate brown (5YR3.5/4) to moderate brown with yellowish (5Y7/4) lateral lunar markings; cephalic sclerites occupying 1/2 (early) to 1/3 (late) length of cephalic division; marginal armature of 10-12 scales anteriolaterally on each median division and 4-5 posteriolaterally; dorsal armature of scattered setae; lateral margins of median divisions sharply angular anteriolaterally, broadly angular posteriolaterally, terminal margin straight; abdominal prolegs 1/3 longer than basal width, slightly constricted

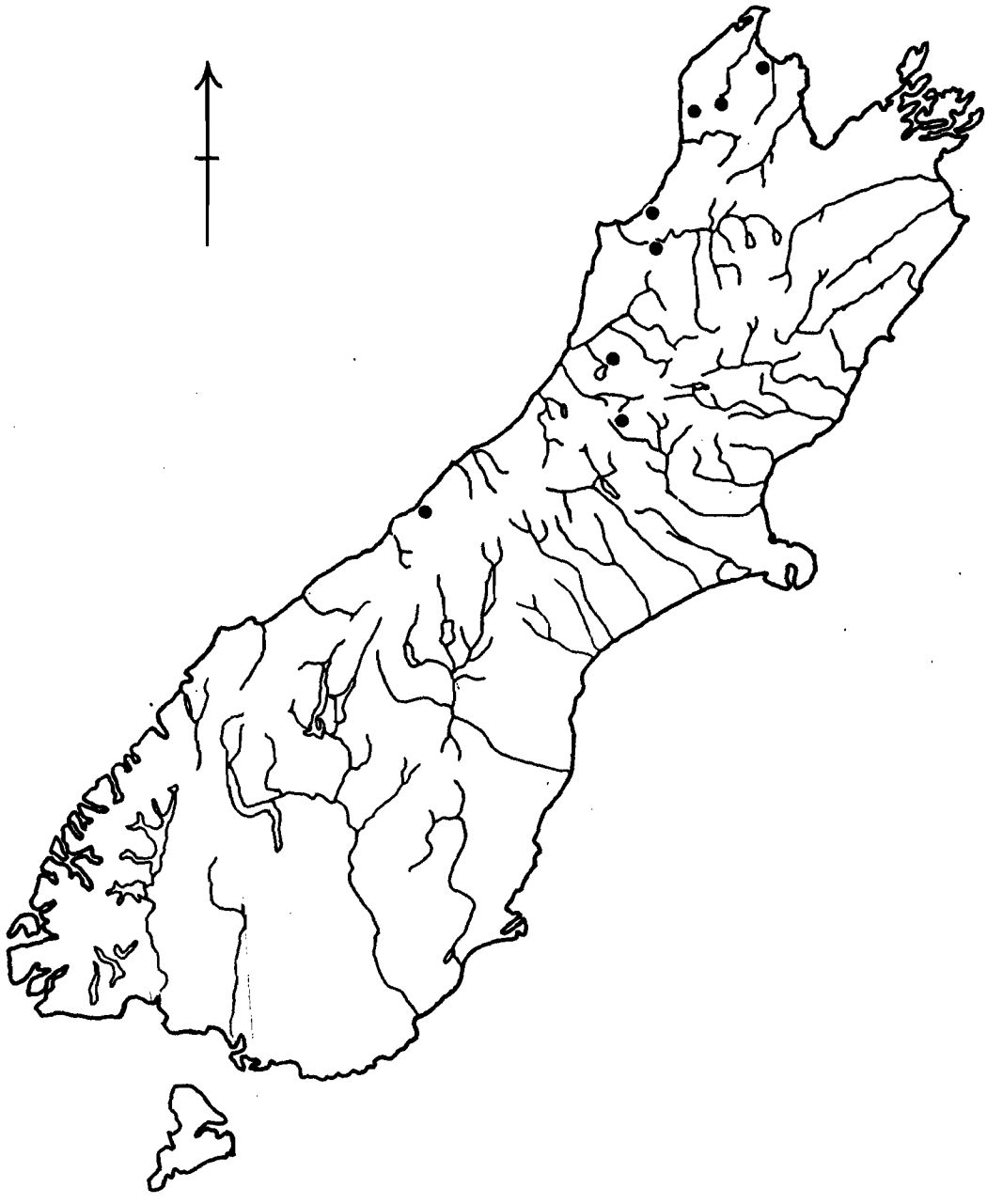


Figure 52. Map of South Island showing localities of *N. tonnoiri*.

sub-basally, bearing dorsally 4-5 clear hairs slightly shorter than proleg, ventral pad occupies 1/4 length of proleg; seventh proleg as long as basal width, bearing apically 3-4 hairs, 3-4 times as long as proleg; anal division separated laterally from fifth median division by shallow subangulate constriction; posterior margin of anal division broadly rounded bearing 7-9 hairs as long as seventh proleg hair, smaller hairs between larger hairs; two tracheal gill filaments per division; posterior anal gill filaments 1/3 size of anterior gill filaments.

Locality Records.

Upper Aorere Valley, Collingwood, L., A. Baker, ?-i-66, Cant. Mus.;

Takaka, A, A.L.Tonnoir, 6-xi-21, Ent. Div. N.;

Waikoropupu Springs, Takaka, S8.171822. L.P.A., V.M.S., 25-x-63, (10), D.A.C., 28-xii-63, (130);

Heaphy Track, Gouland Downs, L.P.A., A.L.Tonnoir, 7-ii-22, Ent. Div. N.; J. Grieve and M. Cross, 10-i-65, Cant. Mus.;

Fairdown Creek, Westport, L., I.D.McLellan, 16-v-65, Cant. Mus.;

Shenandoah Saddle, approx. 1500 ft., L. D.R.C., 22-i-64, Uni.Auck.;

Ten Mile Creek, Buller River, S31. 627162 L.P.A., I.D.McLellan, ?-vii-63, 4-iv-64, 2-v-64, Cant. Mus., V.M.S., 4-iv-64, Cant. Mus.;

Moana, A., A.L.Tonnoir, 16-xii-25, Cant. Mus.;

Lake Brunner, A., A.L.Tonnoir, 5-ii-22, Cant. Mus.;

Tributary of Eel Creek, Lake Brunner, approx. 500 ft., Annon., 31-i-65, Uni. Auck.;

Jack's Hut Stream, Arthur's Pass, L., L.J.D., 28-vii-58, 3-iv-64, Ent. Div. L.;

Waiho River, L., A.L.Tonnoir, 9-i-22, Cant. Mus.;

Docherty's Creek, Waiho River, L., L.J.D., 11-i-60, Ent. Div. L.

N. tonnoiri appears to be restricted to the West Coast of the South Island, extending from Takaka, south to the Waiho River, and east to the Arthur's Pass region. It occurs at altitudes between 500 ft. and 2500 ft. above sea level (Fig. 52). Dumbleton (1963a) stated that it occurred in small cascading streams within bush; however, it has since been collected from deeper, swiftly flowing rivers in the open. It occurs with N. hudsoni, N. campbelli and P. turrifer where the areas of distribution overlap and where suitable habitats occur.

All larval instars of N. tonnoiri and N. chiltoni are very similar, in the shape of the angulate abdominal prolegs, shape of the posterior margin of the anal division, size of the marginal armature and the colour pattern. N. tonnoiri differs from N. chiltoni in not possessing large black spines on the dorsal surface of the fourth instar. The adults of both species vary in detail but are generally very similar, particularly in the venation and shape of the anal angle of the wing. The anal angle of both species is less pronounced than that of other species of N.Z. blepharocerids. The eggs of both N. tonnoiri and N. chiltoni are, apart from size, very similar in shape and colouration (Chp. II. p.5.).

Because the similarities between N. chiltoni and N. tonnoiri are greater than the similarities between them and the other Neocurupira species, it is considered that N. chiltoni and N.tonnoiri are closely related and form a species group.

PERITHEATES Lamb 1912.

Peritheates Lamb, 1912. Trans. N.Z. Inst., 45: 72-73.

Type species P. turrifer.

Campbell, 1921. Trans. N.Z. Inst. 53(as Apistomyia): 258-266;
Tillyard, 1922. N.Z. J. Sci. Tech. 5: 101-107;
Campbell, 1923. Trans. N.Z. Inst., 54: 260-264;
Dumbleton, 1963, N.Z. J. Sci. 6, 2: 234-258.

Tillyard (1922a) andDumbleton (1963a) recognised three species of Peritheates; P. turrifer, P. intermedius and P. harrisi, the latter species being relatively distinct from the former two on size alone. Tillyard separated P. turrifer and P. intermedius on the basis of the ocellar turret shape, the male genitalia and the colour of the abdominal segments. However, the figures supplied by Tillyard of the male genitalia show differences that are dependent on the angle of observation rather than on specific differences, a fact also mentioned by Dumbleton (1963a).

The larvae are practically impossible to distinguish, though Dumbleton (1963a) did attempt to show specific differences.

Adults of P. intermedius collected from the type area (Brooks Stream Reservoir, Nelson), are only just identifiable with any certainty, as the degree of basal constriction of the ocellar turret is not as pronounced as indicated by Tillyard (1922a).

Adult Peritheates collected from the Wangamoa River, Nelson, are impossible to identify definitely as either P. intermedius or P. turrifer, being equally referable to either species if the keys provided by Tillyard are used.

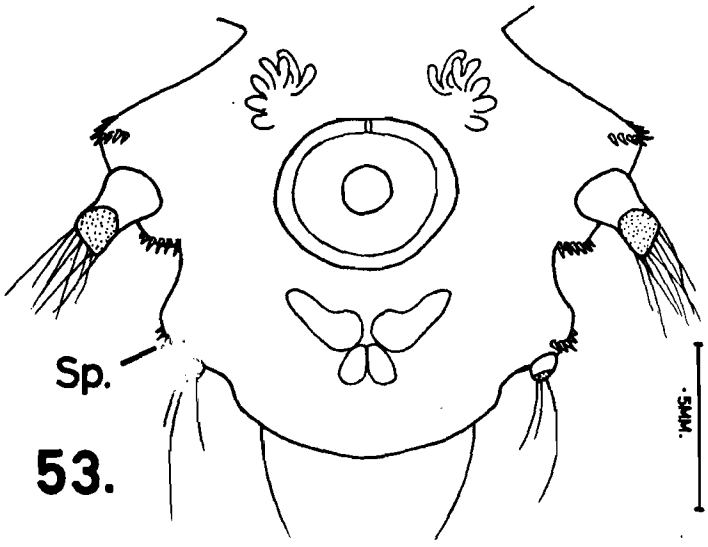
The very close similarity of P. intermedius and P. turrifer in all stages has been mentioned by Dumbleton (1963a), who suggests that these two species may in fact be identical. He has since (pers. comm.) indicated that he now considers the two species to be conspecific.

This view is agreed with here and P. intermedius is placed in synonomy with P. turrifer.

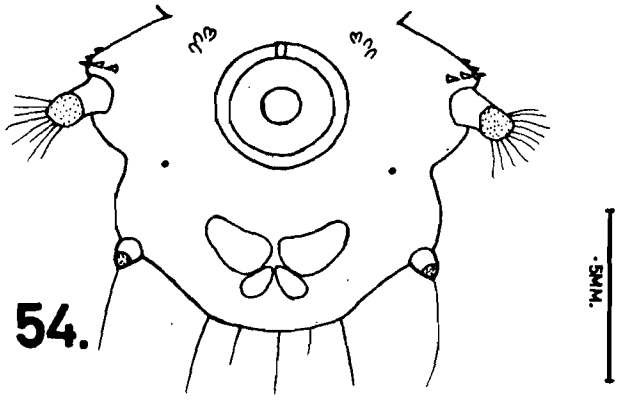
Peritheates turrifer Lamb.

Peritheates turrifer Lamb, 1912. Trans. N.Z. Inst., 45: 72-73;
Campbell, 1921. Trans. N.Z. Inst., 53: 258-266;
Tillyard, 1922, N.Z. J. Sci. Tech., 5: 101-107;
Dumbleton, 1963 , N.Z. J. Sci., 6, 2:234-258.

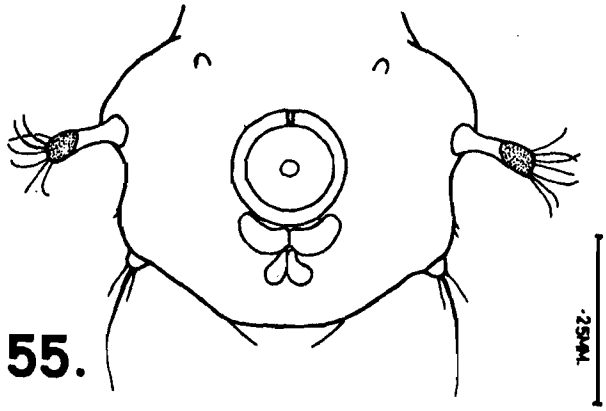
Peritheates intermedius Tillyard, 1922, N.Z. J. Sci.Tech. 5: 101-107;
Tonnoir, 1930, Rec. Indian Mus., 34: 269-175;
Dumbleton, 1963 , N.Z. J. Sci., 6,2: 234-258.



53.



54.



55.

Figures:-

53. Ventral view of posterior end of P. turrifer fourth instar larva.

54. Ventral view of posterior end of P. turrifer third instar larva.

55. Ventral view of posterior end of P. turrifer second instar larva.

Abbreviations:-

Sp. - Spines.

Adult.

Male. Head. Head depth width ratio 1:1.2; eye ratio 1:1.5; vertex width 0.23 times as wide as head width; 12 antennal segments; labial palpi less than three times as long as head depth, first labial palpi segment as long as labrum.

Wing. As in Fig. 4.

Genitalia (Fig. 56b & c). Cercus variable, rounded median concavity, slight indentation laterally.

Female. Head. Head depth width ratio 1:1.2; eye ratio 1:1.9; vertex width 0.33 width of head; 12 antennal segments; labial palpi only slightly longer than head depth, first labial palpi segment shorter than labrum.

Genitalia (Fig. 58a & b). Oviscapt variable;

Internal process of oviscapt conical and rounded apically; oviscapt lobes bearing 8-12 black spines subapically.

Pupa. Length 4.5-5.3. Outer lamellae of pupal gills triangular and pointed, basal width length ratio of outer lamellae 1:2.8.

LARVAE.

Fourth Instar (Fig. 53). Length 4.4-7.0 mm. Sucker width 0.45-0.54 mm. Colour from uniform brownish black (5YR2/1) to moderate brown (5YR4/4) with brownish black patches dorsally on each division; abdominal prolegs bluntly pointed apically, constricted medially; posterior margin of anal division bearing 2 hairs at junction of rounded median and angulate lateral edges.

Third Instar (Fig. 54). Length 3.6-4.1 mm. Sucker width 0.26-0.33 mm. Cephalic sclerites dark brown; remainder body moderate brown (5YR5/4) with darker brown regions mid-dorsally on median divisions, immediate area around dorsal armature spines yellow; cephalic sclerites occupying 1/3 (late) length of cephalic division; marginal armature short dark brown spines irregular arrangement; dorsal armature irregularly arranged short spines, with row of distinct spines across cephalic division posterior to cephalic sclerites; lateral margins of median divisions subangulate anteriolaterally, rounded posteriolaterally; abdominal prolegs twice as long as basal width, constricted medially, bearing dorsally 10-12 fine pale hairs as long as ventral pad, and two thick shorter spines, ventral pad 1/2 as long as proleg; seventh proleg slightly longer than basal width, conical, bearing single hair three times as long as proleg; anal division separated laterally from fifth median division by shallow rounded constriction; posterior margin of anal division broadly rounded medially, slightly concave laterally, bears 2-4 hairs, as long as seventh proleg hair on medial portion; 8 small tracheal gill filaments per division.

Second Instar larvae. (Fig. 55). Length 1.1-2.4 mm. Sucker width 0.15-0.18 mm. Cephalic sclerites dusky brown (5YR2/2); remainder of body varying from uniform moderate brown (5YR3/3) (early) to brownish black (5YR2/1) (late); cephalic sclerites occupying 1/3 (early) to 1/2 (late) length of cephalic division; marginal

armature only on anal division; dorsal armature of small black spines, irregular arrangement, row of 10-12 spines across cephalic division posterior to cephalic sclerites, irregular rows of 12-13 spines on median divisions; lateral margins of median divisions non-angulate, rounded apically; abdominal prolegs twice to three times as long as basal width; bearing dorsally 7-9 fine clear hairs as long as ventral pad, also 1-3 short stout spines, ventral pad 1/3 as long as proleg; seventh proleg as long as wide, bearing a single hair 6-8 times as long as proleg plus two shorter hairs; anal division separated laterally from fifth median division by very shallow rounded constriction; posterior margin of anal division slightly rounded medially, flat to very slightly rounded laterally, bearing two short hairs at junction of lateral and medial edges; two tracheal gill filaments per division.

Locality Records.

The Forks, Hutt River, North Island, A., A. Philpott, ?-i-21, Ent. Div. N.; J. Muggeridge, 16-ii-21, Ent. Div. N.;

Wangamoa River, Nelson, S14. 798367., A., D.A.C., 31-xii-62, 1-i-65. Cant. Mus.;

Nelson, A., A. Philpott, 10-xii-20, Ent. Div. N.;

Coads Creek, Dun Mountain, S20. 687205., L.P.A.; A. Philpott, 21-i-22, 28-x-22, 22-xi-22, 28-xii-22, Ent. Div. N.; D.A.C., 2-xii-61, 29-i-62, 29-xii-62, Cant. Mus.;

Maitai River, Nelson, L.; L.J.D., 23-i-50, Ent. Div. L.;

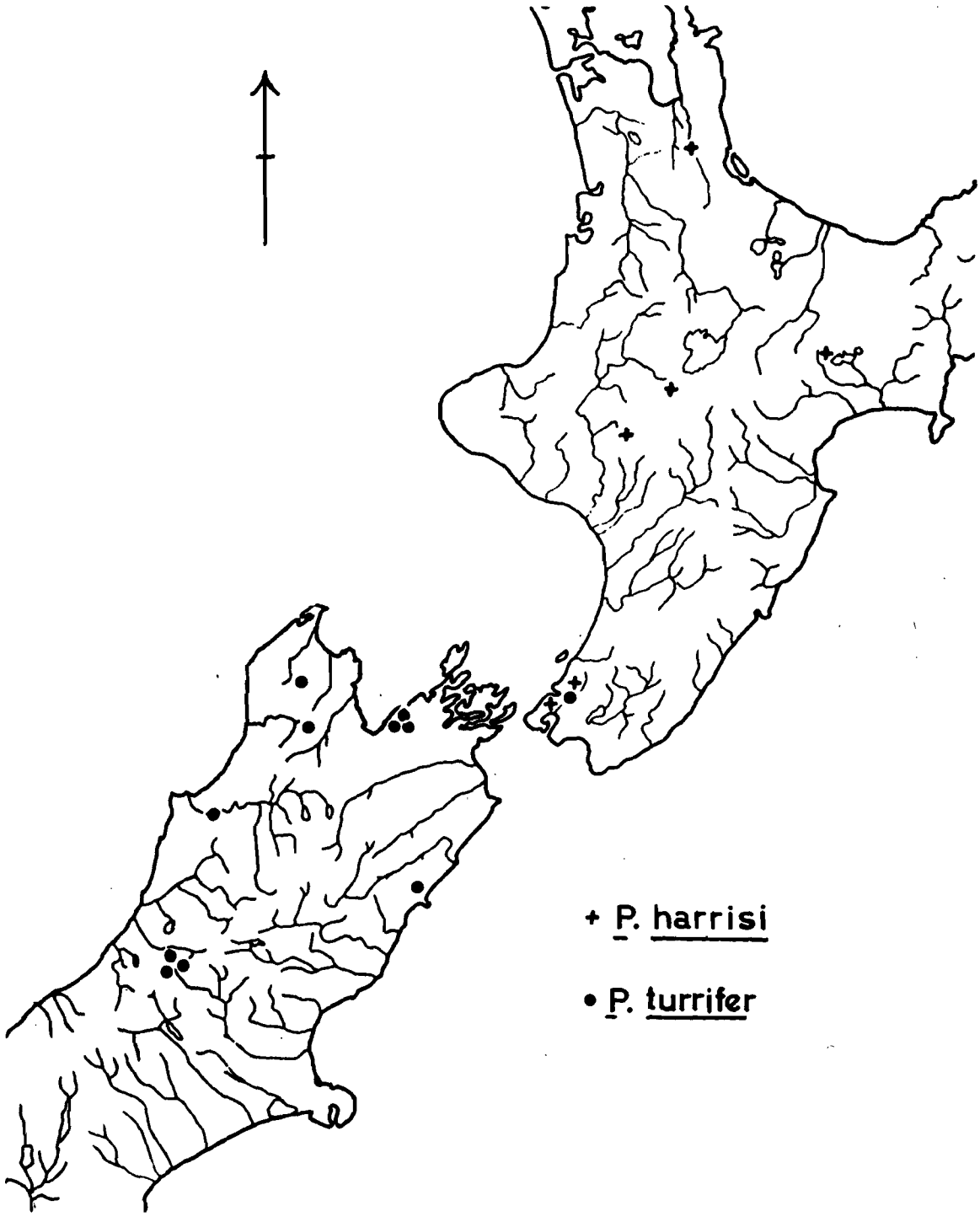

+ P. harrisi
• P. turrifer

Fig. 61. Map of portion of New Zealand showing localities of *P. harrisi* and *P. turrifer*.

Brook Stream Reservoir, Nelson, S20. 638237., L.P.A., R.J.Tillyard, 2-i-22, Ent. Div. N.; D.A.C., 30-xii-64, Cant. Mus.;

Cobb River, Takaka, 2500 ft., L., S.G.Moore, 4-iv-65, Cant. Mus.;

Suicide Creek, Boulder Lake, Takaka, L.P., P.M.Johns & V.M.S., 28-x-63, Cant. Mus.;

Portia Creek, Boulder Lake, 3500 ft., L.P., P.M.Johns, 28-x-63, Cant. Mus.; V.M.S., 28-x-63, (28);

Boyds Creek, Kaikoura, S49. 890988., L.P.A., D.A.C., 29-viii-62, Cant. Mus.;

Ten Mile Creek, Buller River, S31. 162628., L.A., I.D.McLellan, 2-iv-64, Cant. Mus.;

Warnock's Nob, Otira, A., G.V. Hudson, 5-xii-08, Dom. Mus.;

Otira, A., A.L.Tonnoir, 9-ii-22; T.Harris, Cant. Mus.;

Otira Valley, S59. 050337, 2800 ft., A., D.A.C., 23-ii-63, Cant. Mus.;

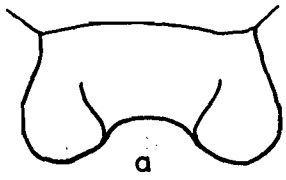
Pegleg Creek, Arthur's Pass, S59. 055340., L.P.A., D.A.C., 15-xii-62, Cant. Mus.;

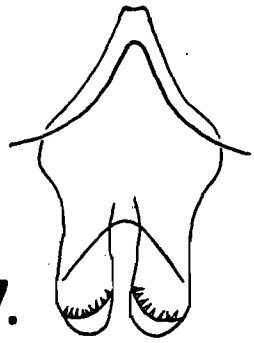
Arthur's Pass, A., G.V.Hudson, ?-xii-22, Dom. Mus.;

Bealey Chasm, Arthur's Pass, S59. 050313., 2750 ft., D.A.C., 1962-1965, Zoology Dept. University of Canterbury;

Jack's Hut Stream, Arthur's Pass, S59. 053311., 2500 ft. L., L.J.D., 13-iv-62, Ent. Div. L.; D.A.C., 20-xi-63, Cant. Mus.;

Avalanche Creek, Arthur's Pass, S59. 054285., 2500 ft., D.A.C., 4-i-62, Cant. Mus.





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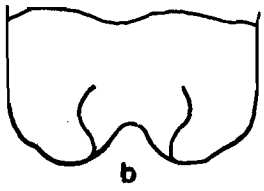

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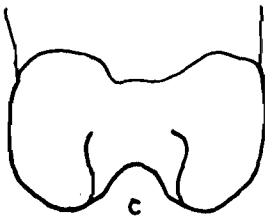

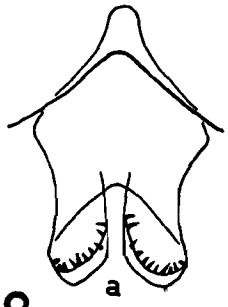

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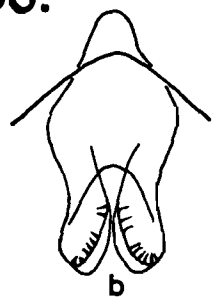
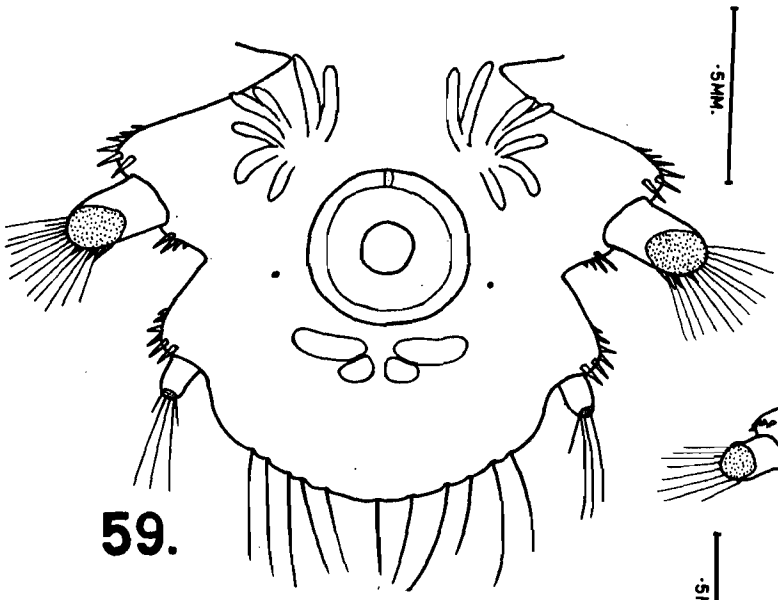
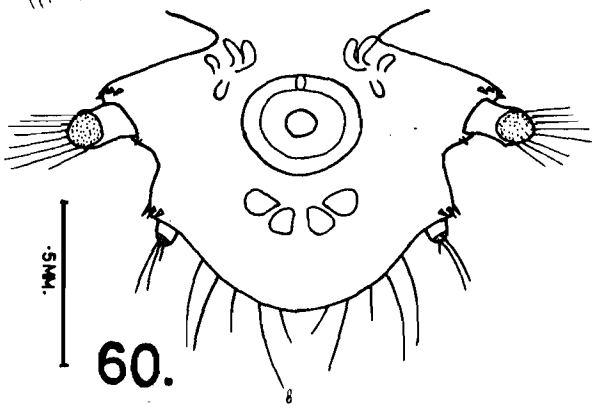




59.



60.

This species is of special interest in that it is the only New Zealand blepharocerid to occur in both North and South Islands (Fig. 61). It is known from only the southern tip of the North Island, but in the South Island has been collected extensively in the Nelson and Arthur's Pass regions. The distribution of P. turrifer in the area between Nelson and Arthur's Pass, is poorly known.

P. turrifer occurs mainly in small torrential bush covered streams, but is also found in larger, open, stable rivers. It is known to occur with N. hudsoni, N. campbelli and N. tonnoiri where conditions are suitable and the areas of distribution overlap. It has an altitudinal distribution of between 200 ft. and 300 ft. above sea level.

Peritheates harrisi (Campbell)

Apistomyia harrisi Campbell, 1921, Trans. N.Z. Inst., 53: 262-263.
Peritheates harrisi Tillyard, 1922, N.Z. J. Sci. Tech., 5: 101-107; Campbell, 1923, Trans. N.Z. Inst., 54: 260-264; Dumbleton, 1963, N.Z. J. Sci., 6, 2, 234-258.

Adults.

Male. Head. Head depth width ratio 1:2; eye ratio 1:1.7; vertex width 0.19 times as wide as head width; 12 antennal segments; labrum longer than first segment of labial palpi; labial palpi three times as long as head depth.

Genitalia (Fig. 56a). Cercus wide, very shallow median concavity.

Female. Head. Head depth width ratio 1:2.2; eye ratio 1:2; 12 antennal segments; labial palpi twice as long as head depth, second segment shorter than labrum.

Genitalia (Fig. 57). Internal process of oviscapt concave apically, oviscapt lobes bearing 8-10 clear spines subapically.

Pupa. Length 4.9-6.0 mm. Outer lamellae of pupal gill longer than P. turrifer, more rounded apically; basal width length ratio 1:3.1.

LARVAE

Fourth Instar (Fig. 59). Length 4.3-8.1 mm. Sucker width 0.47-0.54 mm; cephalic sclerites black; remainder of body uniformly yellowish brown (10YR3/2); posterior margin of anal division bearing 9-10 hairs, inset at bases.

Third Instar (Fig. 60). (1 specimen only). Length 4.0 mm. Sucker width 0.35 mm. Cephalic sclerites black; remainder of body moderate brown (5YR4/4) with dorsal median moderate brown (5YR3/4) patches; cephalic sclerites occupying 1/3 length of cephalic division; marginal armature short sharp clear spines; dorsal armature short sharp black spines irregularly arranged laterally, also as irregular rows across anterior and posterior of median divisions; lateral margins of median divisions subangulate anteriolaterally, less angulate posteriolaterally; abdominal prolegs longer than basal width, rounded apically, constricted medially,

bearing dorsally 2-3 spines plus numerous fine pale hairs longer than ventral pad, ventral pad 1/2 as long as proleg; 7th proleg as long as basal width, bearing 3-5 hairs 1½ times as long as proleg; anal division separated laterally from fifth median division by shallow subangulate constriction; posterior margin of anal division broadly rounded medially, slightly concave laterally, bearing 4-5 irregularly placed larger hairs and 5-6 smaller hairs medially; 8 tracheal gill filaments per division; anal gill filaments small.

Second Instar. No material available. Probably very similar to P. turrifer

Locality Records.

Te Aroha, A., Annon., 1-iii-23, Cant. Mus.;

Waiorongomai Stream, Te Aroha, L., P.M.Johns, 14-i-64, Cant. Mus.;

Makau Stream, Lake Waikare Moana, 2220 ft., L.P., M. Winterbourne, 28-iii-64, Cant. Mus.; J. McLean, 31-iii-64, Uni. Auck.;

Whakapuparui Stream, Chateau Tongariro, L., M. Winterbourne, ?-v-64, Cant. Mus.;

Waipuna Stream, National Park, L., D.R.Cowley, 23-ii-65, Uni.Auck.;

Ohakune, L.A., A.L.Tonnoir, 8-iii-23, Cant. Mus.; L.J.D., 13-x-60, Ent. Div. L.;

Akatarawa River, L., L.J.D., 11-x-60, Ent. Div. L.;

Mathew Stream, Wellington L.P., S.G.Moore, ?-vi-65, Cant. Mus.

This species is known at present only from the North Island (Fig.61), and collections indicate that it could be widely spread throughout the mountainous areas of the North Island. Little is known about the habitat of this species, Dumbleton stated that it occurs in bush-covered streams. It has an altitudinal distribution of between 500 ft. and 2250 ft. above sea level.

Larval Abnormalities.

Larvae of New Zealand species of blepharocerids are very uniform in their morphology throughout their areas of distribution. This may be the result of serious defects or mutations being removed from the population by the rigorous habitat preferred by the larvae.

Larvae collected from frequently flooded streams often show scar-marks on the dorsal surface. These are probably the result of stone damage. The scars are quite distinct from the following abnormalities:-

N. campbelli.

Fourth Instars.

1. Loss of 2/3 of right side of both 5th median and anal divisions.
2. Posterior margin of anal division shallowly concave medially; black posterior hairs absent.

N. chiltoni.

Fourth Instars.

1. Posterior margin of anal division notched medially;

strong posterior hairs absent from notched area.

2. Loss of 2/3 of right side of both 5th median and anal divisions.

N. hudsoni.

Fourth Instar.

Complete loss of right 7th abdominal proleg; only one posterior anal gill filament, the latter being placed medially.

Second Instar.

Complete loss of left 7th abdominal proleg.

P. turrifer.

Third Instar.

Left 7th abdominal proleg displaced anteriorly to constriction between fifth median and anal divisions; proleg protruding at right angles to body axis, similar in shape to first instar proleg.

These abnormalities could be predator damage but,

because of the similarities of these abnormalities, it is considered that they are of a genetic nature and that they may give some idea as to how the very reduced Anal Division has evolved in some of the larvae of the Edwardsinae and the specialised Apistomyia.

KEY TO THE ADULTS OF AUSTRALASIAN GENERA OF BLEPHAROCERIDAE

(1). Maxillary palpi 4-5 segmented; eyes not divided; dichoptic in both sexes; wing with Rs and M veins three branched.

----- Edwardsina Alexander.

Maxillary palpi 1-2 segmented; eyes divided, holoptic or dichoptic in males; wing with Rs vein forked or simple, median vein with only M1 and M4 present.

----- (2).

(2). Rs vein forked.

----- Neocurupira Lamb (3).

Rs vein simple.

----- (4).

(3). Ocellar turret prominent; 14 antennal segments, maxillary palpi short.

----- subgenus Neocurupira Lamb. (New Zealand).

Ocellar turret small; 12 antennal segments; maxillary palpi elongate.

----- subgenus Austrocurupira Dumbleton. (Australia).

(4). Rs vein nearly straight, ending just above wing apex; male eyes dichoptic.

----- Peritheates Lamb

Rs vein curving upwards, ending close to R1; male eyes holoptic.

----- Apistomyia Bigot

KEY TO ADULTS OF NEW ZEALAND NEOCURUPIRA

1. Labial palpi short in both sexes, sub-equal to head-depth; antennae 11 or 12 segmented, distal segments wider than long; microtrichia dense, female wings brachypterous or macropterous; internal process of oviscapt conical; male dichoptic, eye ratio 1:2.0.

-------- N. campbelli Dumbleton.

Labial palpi long in both sexes, 1.5-2 times as long as head-depth; antennae 14-15 segments, moniliform; wings clear; female always macropterous; internal process of oviscapt conical or truncate; male holoptic or dichoptic.

-------- (2)

2. Antennae 14 segmented; males holoptic or dichoptic, eye ratios from 1:1.4 -1:0.5; dististyles widest at midlength; posterior margin of cercus notched basally; internal process of oviscapt truncate, apex concave.

-------- hudsoni-complex.

(N. hudsoni proper = male holoptic, eye ratio 1:0.5)

Antennae 15 segmented; male dichoptic, eye ratio 1:1.6 or 1:0.9; dististyles not widest at midlength; posterior margin of cercus deeply or broadly concave; internal process of oviscapt conical.

-------- (3).

(3.) Male eye ratio 1:0.9; anal angle of wing approximately 120°, not prominent; vein 1A not reaching wing margin; internal process of oviscapt conical, constricted apically, oviscapt lobes bearing fine pale setae subapically.

-------- N. chiltoni (Campbell)

Male eye ratio 1:2.1;anal angle of wing approximately 110°; vein 1A reaching wing margin; internal process of oviscapt conical, oviscapt lobes bearing short dark setae subapically.

-------- N. tonnoiri Dumbleton.

KEY TO THE ADULTS OF NEW ZEALAND PERITHEATES

(1) Male ocellar turret rounded; wing length approximately 8 mm; cercus wide with shallow median concavity; female with interior process of oviscapt truncate, slightly concave apically, oviscapt lobes bearing 8-10 clear spines subapically.

-------- P. harrisi (Campbell).

Male ocellar turret constricted or diverging basally; wing length approximately 6 mm; cercus with slight lateral flattening, median concavity rounded; female with interior process of oviscapt rounded apically, oviscapt lobes bearing 5-13 black spines subapically and at approximately mid length.

-------- P. turrifer Lamb.

KEY TO LARVAL INSTARS OF NEW ZEALAND BLEPHAROCERDAE

The method utilized by Campbell (1921 & 1923) and Dumbleton (1963a) to distinguish the larval instars of N. chiltoni can be used with suitable modification for all known New Zealand species.

(1) Tracheal gill filaments absent; antennae one segment; egg-burster on cephalic sclerites; sucker width 0.057-0.067 mm.
-------- First Instar (refer to N. chiltoni.)

Tracheal gill filaments present, antennae two segmented; no egg-burster. -------- (2).

(2) Two tracheal gill filaments per body division; sucker width 0.14-0.24 mm. -------- Second Instar.

More than two tracheal gill filaments per body division.
-------- (3).

(3) Eight tracheal gill filaments per body division; sucker width 0.26-0.44 mm. -------- Third Instar.

Fourteen tracheal gill filaments per body division; sucker width 0.47-0.83 mm. -------- Fourth Instar.

KEY TO FOURTH INSTAR LARVAE OF NEW ZEALAND BLEPAHAROCERIDAE

(1) Marginal armature of scales; dorsal armature without spines or if present very large; abdominal prolegs with pale hairs only; posterior margin of anal division broadly rounded, bearing 6-30 hairs, row of short setae ventral to margin.
-------- genus Neocurupira Lamb -- (2).

Marginal armature of irregular dark pointed spines; dorsal armature of small blunt spines; abdominal prolegs with 1-3 short dark spines dorsally among paler hairs; posterior margin of anal division rounded medially, constricted and angulate laterally, bearing 1-6 hairs medially, without row of short setae ventral to margin.

-------- genus Peritheates Lamb -- (5).

(2) Abdominal prolegs pointed apically, angulate laterally, constricted basally; anal division separated laterally from 5th median division by acute angulate constriction, posterior margin thin.

-------- (3).

Abdominal prolegs rounded apically, not angulate laterally, not constricted basally, with slight medial constriction; anal division separated laterally from 5th median division by non-angulate constriction, posterior margin thicker.

-------- (4).

(3) Dorsal armature of regularly arranged large black spines; seventh abdominal proleg pointed apically, constricted basally, 2-4 dark hairs dorsally; sucker width 0.60 - 0.65 mm.

-------- N. chiltoni (Campbell).

Dorsal armature without large spines; seventh abdominal proleg rounded apically, not constricted basally, without dark hairs dorsally; sucker width 0.54-0.64 mm.

-------- N. tonnoiri Dumbleton.

(4) Posterior margin of anal division bearing approximately 30 hairs; anal division separated laterally from 5th median division

by shallow constriction; colour varying from uniform light brown to highly patterned; sucker width 0.60-0.83 mm.

-------- hudsoni = complex.

Posterior margin of anal division bearing 6-8 black hairs; anal division separated laterally from 5th median division by very shallow constriction; colour uniformly dusky yellowish brown; sucker width 0.48-0.59 mm.

-------- N. campbelli Dumbleton.

(5) Posterior margin of anal division bearing 6-8 hairs medially, hair bases inset, appearance crenulated; abdominal prolegs rounded apically, slightly constricted medially; 7th abdominal proleg longer than basal width; sucker width 0.47-0.54 mm.

-------- Peritheates harrisi (Campbell).

Posterior margin of anal division bearing 2 hairs at junctions of rounded median and angulate lateral edges; hair bases not inset; abdominal prolegs bluntly pointed apically, constricted medially; 7th abdominal proleg shorter than basal width; sucker width 0.45-0.54 mm.

-------- P. turrifer Lamb.

KEY TO THIRD INSTAR LARVAE OF NEW ZEALAND BLEPHAROCERIDAE

(1) Marginal armature of scales.

-------- genus Neocurupira (2).

Marginal armature of dark pointed spines.

-------- genus Peritheates (5).

(2) Abdominal prolegs constricted medially, angulate laterally; 7th proleg longer than basal width; posterior margin of anal division bearing 18-23 strong dark hairs.

-------- (3).

Abdominal prolegs only slightly constricted medially, not angulate laterally; 7th proleg shorter than basal width; posterior margin of anal division bearing 6-8 hairs.

-------- (4).

(3) 7th abdominal proleg inset basally, roundly truncate apically; anal division separated laterally from 5th median division by deep angulate constriction; sucker width 0.26-0.32 mm.

-------- N. tonnoiri Dumbleton.

7th abdominal proleg not inset basally, cone shaped; anal division separated laterally from 5th median division by shallow angulate constriction; sucker width 0.30-0.36 mm.

-------- N. chiltoni (Campbell).

(4) Prolegs rounded apically; anterior filaments of anal gills larger than posterior gill filaments and curving around 6th sucker; anal division separated laterally from 5th median division by deep subangulate constriction; sucker width 0.35-0.44 mm.

-------- hudsoni-complex.

Prolegs slightly pointed apically; anterior and posterior anal gill filaments subequal in size; anal division separated laterally from 5th median division by very shallow constriction; sucker width 0.30-0.36 mm.

-------- N. campbelli Dumbleton.

(5) Posterior margin of anal division broadly rounded medially, slightly concave laterally, bearing 8-12 hairs; 7th proleg rounded apically; anterior and posterior anal gill filaments subequal in size; sucker width 0.35 mm. (only two specimens).

-------- Peritheates harrisi (Campbell)

Posterior margin of anal division only slightly rounded medially, lateral edges slightly concave, bearing 2-4 hairs; 7th proleg conical, pointed apically; anterior anal gill filaments larger than posterior filaments; sucker width 0.26-0.33 mm.

-------- P. turrifer. Lamb.

KEY TO SECOND INSTAR LARVAE OF NEW ZEALAND BLEPHAROCERIDAE

(1) Posterior margin of anal division bearing 8-22 hairs; abdominal prolegs robust; marginal armature if present of scales.

-------- genus Neocurupira. (2).

Posterior margin of anal division bearing 2 hairs; abdominal prolegs thin, constricted medially; marginal armature of dark, sharp spines.

-------- genus Peritheates. (5).

(2) 6th abdominal proleg slightly constricted medially, curving posteriorly; posterior margin of anal division bearing 16-22 hairs; marginal armature prominent.

-------- (3).

6th abdominal proleg not constricted medially, cone shaped; posterior margin of anal division bearing 7-14 hairs; marginal armature small or absent.

-------- (4)

(3) 6th abdominal proleg twice as long as basal width; 7th proleg hemispherical; posterior margin of anal division flattened laterally, very slightly pointed medially; anal division separated laterally from 5th median division by deep angulate constriction, close to base of 6th proleg; sucker width 0.18-0.19 mm.

-------- N. chiltoni (Campbell)

6th abdominal proleg 1/3 as long as basal width; 7th proleg conical; posterior margin of anal division broadly rounded; anal division separated laterally from 5th median division by subangulate constriction not close to base of 6th proleg; sucker width 0.14-0.18 mm.

-------- N. tonnoiri Dumbleton.

(4) Posterior margin of anal division rounded apically, slightly concave laterally, bearing 12-14 hairs; 6th proleg as long as basal width, rounded apically; 7th proleg conical, not prominent; posterior anal gill filament 1/3-1/2 as long as anterior filament; anal division separated laterally from 5th median division by subangulate constriction; sucker width 0.20-0.24 mm.

-------- hudsoni-complex.

Posterior margin of anal division broadly rounded, continuing anteriorly beyond 6th proleg, bearing 7-9 short black hairs; 6th

proleg as long as basal width, conical, sharply rounded apically; 7th proleg conical prominent; posterior anal gill filaments 2/3 as long as anterior filaments; sucker width 0.17-0.18 mm.

-------- N. campbelli Dumbleton.

(5) Marginal armature of short dark spines only on anal division; 7th proleg conical, bearing a single clear hair; abdominal prolegs 2.5 times as long as basal width, constricted laterally; sucker width 0.15-0.18 mm.

-------- Peritheates turrifer Lamb.

Second instar material of P. harrisi not available.

The Origin and Evolution of the Australasian Blepharoceridae

Because the Blepharoceridae are in almost all stages of their life cycle dependent on fast flowing water, Tillyard (1922b) believed that the dispersal of this family took place along definite land bridges, not by sea or air carriage, and Edwards (1929) believed the family to be of special value in zoogeography. However, Edwards pointed out that blepharocerids are known from isolated volcanic islands and suggested that some migration by sea routes may occur. The distribution and affinities of Neocurupira chiltoni suggests that aerial colonization is also possible. Even so it is agreed here that the main dispersal routes of the Blepharoceridae were probably along land bridges.

From a study of the morphology of the family, Tillyard (1922b) considered that the Blepharoceridae arose in Jurassic times. Alexander (1958, 1963), despite a lack of fossil evidence, on the basis of the virtual world-wide distribution of the Blepharoceridae, suggested that the family originated during the mid-Mesozoic or

even earlier during the Permian.

The following is an attempt to explain the origin and evolution of the Australasian and in particular New Zealand blepharocerids and is summarized in Figure 62.

The Australasian blepharocerids belong to the subfamilies Edwardsininae and Apistomyiinae.

Origin of Edwardsininae: Tillyard (1922b), Tonnoir (1922a), Kitakami (1950) and Alexander (1958 and 1963) considered that the primitive Edwardsininae (maxillary palpi long; eyes undivided; wings with veins Rs and M both three-branched) were ancestral to the remainder of the Blepharoceridae (maxillary palpi reduced; eyes divided; wing venation reduced). However, Edwards believed that it was unwarranted to assume an ancestral nature for Edwardsina; more recently, Stuckenberg (1958) after examining the affinities of Edwardsina and Paulianina with other Blepharoceridae, concluded that it is incorrect to consider the Edwardsininae as ancestral to the remainder of the family.

The distribution of the Edwardsininae (South Africa, South Australia, Tasma nia and South America) may be taken to suggest a southern origin for this subfamily. Hennig (1960) considered that that the affinities of the present subgenera of Edwardsina also suggest a southern origin in Antarctica, but reserved judgement until there has been further detailed systematic research. Tillyard (1922b) believed that the then known distribution of Australian blepharocerids could best be explained by the evolution of the Blepharoceridae in a temperate Antarctica. Tonnoir (1930c) also believed that the Australian Edwardsina was of southern origin.

However, Darlington (1965), after reviewing the probable climatic history and present distribution of significant plants and animals on the lands surrounding it now, concludes that the Antarctic Continent was not an important centre of evolution and Stuckenberg (1958), from his considerations of the affinities of the Edwardsininae and the other Blepharoceridae, considered that the centre of

origin of the Edwardsininae was not southern but more probably in the Northern Hemisphere. Dumbleton (1963b) figured the Australian Edwardsina as arriving from the Northern Hemisphere.

If in fact the Australian Edwardsina did come from the north, then the present distribution of the Australian blepharocerids * could best been explained by Edwardsina arriving in Australia when Tasmania was still connected to the mainland. Followed by the more specialized blepharocerids which arrived after the Oligocene when Tasmania had become an island (Darlington 1965).

(* Edwardsina found in Tasmania and Australia, Apistomyia and Neocurupira (Austrocurupira) found only in Australia).

These suggestions are similar to those of Ross (1956) who believed that there have been two invasions of mountain caddisflies into Australia. The first, of primitive genera, arrived during the late Mesozoic when the Malay Archipelago was probably an extensive land mass connected intermittently with New Guinea at the same time as Australia was connected to New Guinea. Ross considers that the second invasion, consisting of more specialized genera, entered Australia during the Miocene through island chains between south-eastern Asia, New Guinea and Australia. It is possible that, as well as the primitive caddisflies, Edwardsina arrived in Australia during the Cretaceous, with the Apistomyiinae and the more specialized caddisflies arriving during the Miocene.

Though believing Edwardsina to be ancestral, Tonnoir (1930a) considered that its absence from New Zealand and the distribution of the other Australasian blepharocerids indicated a northern origin for New Zealand blepharocerids. Dumbleton (1963a and 1963b), on the basis of blepharocerid and similiid distributions, also considered the New Zealand blepharocerids to have come from the north.

According to Ross (1965), Fleming (1962) and Suggate (1963) New Zealand was probably connected to the north through New Caledonia by land or island chains during the Cretacecus. It is considered that Edwardsina colonized Australia during this period. Why

Edwardsina failed to reach New Zealand remains unexplained, but it is possible that the New Zealand land connections were later in the Cretaceous after Edwardsina had already reached Australia and more specialized blepharocerids were migrating southwards.

The possible origin of the Blepharoceridae in the Northern Hemisphere with the most primitive forms (Edwarsininae) existing in the southernmost land extensions of the Southern Hemisphere is in general agreement with Darlington (1965) who believed that evolution and dispersal run generally from large to small land masses. The presence of the Edwardsininae in the Southern Hemisphere could be regarded as the result of southerly migration from the northern centre of origin with the northern stock now extinct. In principle this is similar to the hypothetical scheme proposed by Darlington for the carabid beetles.

Origin of Apistomyiinae: This subfamilly includes all the remaining Australasian blepharocerids.

Because he believed the Edwardsinae were ancestral, Tillyard (1922b) considered that the Australasian Apistomyiinae were of a southern origin. However, Tonnoir (1930a), because of the comparatively specialized Apistomyia species in Australia and the absence of Edwardsina from New Zealand, believed that the Australasian Apistomyii nae were from the north. Dumbleton (1963a) agreed that Apistomyia may have a northern origin, but offers an alternative suggestion that the Apistomyia may have arisen in Australia from Neocurupira and then migrated north. It is believed here, however, that the present distribution of Apistomyia* is the result of an Asian origin rather than an Australian origin.

(*Corsica, Cyprus, Northern India, Eastern Australia, Formosa and Japan.)

According to Dumbleton (1963a) Tillyard regarded Neocurupira as giving rise to Apistomyia and Peritheates. Morphologically this

view is logical if it is accepted that Peritheates has lost vein R2+3 and Apistomyia vein R4+5, though the curved formation of vein R2+3 in Apistomia is difficult to explain.

The possibility of Neocurupira having given rise to the Apistomia is weakened by the evidence of distribution of Neocurupira (Australia and New Zealand) and of the absence of Apistomyia in New Zealand. Rather, this suggests that Neocurupira is a relict group with northern ancestors. Because Neocurupira nicholsoni Tillyard, possesses larvae very similar to those of Apistomyia, Tonnoir (1930a) was not at all satisfied that N. nicholsoni was congeneric with the genotype of Neocurupira. Dumbleton (1963a) placed N. nicholsoni in the subgenus Austrocurupira. Because there is no geological evidence for a direct Trans-Tasman land bridge at any time (Fleming 1962), it would be safer to consider N. nicholsoni as belonging to Apistomyia, though retaining the ancestral holoptic eyes and forked Rs vein. However, until further studies are undertaken on the affinities of the Australasian Neocurupira, the status of Austrocurupira Dumbleton remains unchanged. The similarities in larval form of Apistomyia and N. nicholsoni suggest that the latter may have arrived in Australia during the Miocene with Apistomyia and thus has no direct link with New Zealand Neocurupira which arrived during the late Cretaceous.

Dumbleton (1963a and 1963b) considered that the simple Rs vein of Peritheates is due to the loss of R2+3 and that Peritheates segregated from Neocurupira stock within New Zealand. The present distribution of Peritheates interpreted in the light of past geological changes in New Zealand makes this suggestion highly acceptable.

Evolution of New Zealand Blepharocerids: During the mid-Eocene New Zealand was still a single land mass, but by the Oligocene was transgressed by the sea to such an extent that two islands resulted, one lying over the north-east of the present North Island, the other

reaching from the middle of the present South Island to the south of Stewart Island. According to Fleming (1962) there is evidence that much of New Zealand at this time was peneplained and very low lying, with some mountains present in the south. How blepharocerids managed to survive this period with its probably sluggish streams and rivers is difficult to suggest, but it may be significant that N. chiltoni can at the present survive in water very much slower than that normally tolerated by other species.

It is considered that, during this period, when New Zealand first consisted of two islands, Peritheates separated from the ancestral stock by evolution of dichoptic-eyed males and the loss of vein R2+3. The present distribution of the genus Peritheates strongly suggests that it arose in the then northern island, Neocurupira retaining the more primitive characters in the southern island.

New Zealand again became a single land mass during the Lower Miocene, lying approximately over the present position of New Zealand. Fleming (1962 and 1963) believed that the Miocene in New Zealand was warmer than was any previous age and that the alpine zone (between tree-line and permanent snow) did not exist in New Zealand at that time. What effect the higher temperatures would have had on the blepharocerids of that time is not known, but it is significant that blepharocerids exist in the tropics at present. It is possible that some of the blepharocerids took refuge in the then southern-most land extension, with the alpine flora (Wardle 1963). It is assumed that during this period Peritheates migrated south and that Neocurupira, because of having evolved in the cooler south, was prevented from migrating north to any great extent.

During the Upper Miocene there is evidence (Fleming, 1962) that temperatures were cooler and that considerable faulting of the land mass in the Marlborough area took place. Why Neocurupira did not manage to migrate north is difficult to explain, but it is not found in the present North Island and would appear to have reached

the Marlborough Sounds after the present Cook Strait was formed during the Pliocene-Pleistocene.

During the early Pliocene New Zealand again consisted of two islands. The South Island was of approximately the present configuration but extended across the present Cook Strait on to the southwestern tip of the present North Island. A shallow sea separated this peninsula from the northern part of the North Island (Fleming 1962). It is considered that during this period Peritheates harrisi evolved in the then North Island and P. turrifer in the then South Island. It is further postulated that when the present Cook Strait was formed during the Pliocene-Pleistocene a small population of P. turrifer was isolated from the South Island; and that, when the shallow sea regressed off the centre of the North Island, P. harrisi migrated south until now it is found in the small southern area of the North Island inhabited by P. turrifer.

The presence on Banks Peninsula of N. chiltoni, the only New Zealand blepharocerid to have large black spines on the fourth instar larva, is extremely interesting. This peninsula is a remnant of two extinct volcanic cones and, according to Liggett and Gregg (1965), was probably initially active during the Cretaceous. It was active during the Pliocene-Pleistocene, with very restricted activity during the Pleistocene-Holocene. The volcanoes were separated from the main South Island until approximately the last volcanic activity when they were connected to the mainland by low aggraded plains. As the last volcanic activity was very limited Banks "Peninsula" was probably available for colonisation by blepharocerids during the Pleistocene. Dumbleton (1963a) considered that N. chiltoni evolved from aerial colonists as the aggraded Canterbury Plains do not provide suitable ecological conditions for invasion by water.

Apart from the large spines on the fourth instar larva of

N. chiltoni this species is very similar in egg shape, larval morphology and general adult morphology to N. tonnoiri. Therefore it is considered that the aerial colonists of Banks Peninsula were of the tonnoiri-type. The nearest that N. tonnoiri is known to approach Banks Peninsula is Arthur's Pass, a direct distance of 70 miles. If the prevailing winds were westerly during the Pleistocene as suggested by Gage (1964), it is quite probable that the original colonists could have been blown the intervening distance.

However, if blepharocerid adults can become aerial colonists it is surprising that other species of blepharocerid occurring at Arthur's Pass have not found their way to Banks Peninsula.

Mount Egmont, Taranaki, North Island, is very similar to Banks Peninsula in that it is a recently extinct volcanic dome separated from the main mountain chain and the known blepharocerid localities, by ecologically unsuitable terrain. Despite intensive searching by a number of collectors, no blepharocerids have yet been discovered, though both L. J. Dumbleton and A. G. McFarlane (pers. comm.) indicate that other freshwater fauna is abundant on the mountain. Being located to the west of blepharocerid localities Mount Egmont has poor chances of aerial colonisation from the predominantly westerly winds.

During the Last Pleistocene Glaciation, Mount Egmont was connected to the north-west of the South Island by a flat aggraded plain, probably similar to the present Canterbury Plains. This ecologically unsuitable terrain was no doubt the main reason that no South Island blepharocerids reached the North Island, and vice versa, during this period.

The present distribution of the remaining Neocurupira species makes it difficult to form a hypothesis concerning their pattern of evolution.

It seems likely that the original hudsoni-complex stock became separated into two or possibly three populations, some time after the Oligocene or perhaps during the Pliocene-Pleistocene periods. The separation, which has given rise to N. hudsoni and the "southern" forms, appears to have taken place after the evolution of the

commensal chironomid association, as it is unlikely that such an association would evolve twice.

The known distribution of N. hudsoni and Form D strongly suggests that the populations of these two blepharocerids have only very recently regained contact, probably since the retreat of the ice at the end of the Last Pleistocene Glaciation. The evolutionary stages between the holoptic eyes and long labial palpi of N. hudsoni and the dichoptic eyes and short labial palpi of Form D are suggested by the series:- N. hudsoni, Form A, Form B, Form C and Form D.

The distribution of N. campbelli suggests that this species has been associated with N. hudsoni for a considerable time, for, apart from an altitudinal restriction, its geographic range practically coincides with that of N. hudsoni. Neocurupira campbelli is the only other New Zealand blepharocerid which tolerates the commensal chironomid Dactylocladius commensalis and this suggests two possible origins for N. campbelli. Firstly, that N. campbelli separated early from the hudsoni-complex stock just as the chironomid association was developing and no further development took place, or secondly, and considered here as less likely, that there is no close relationship and that the chironomid association is at present just developing.

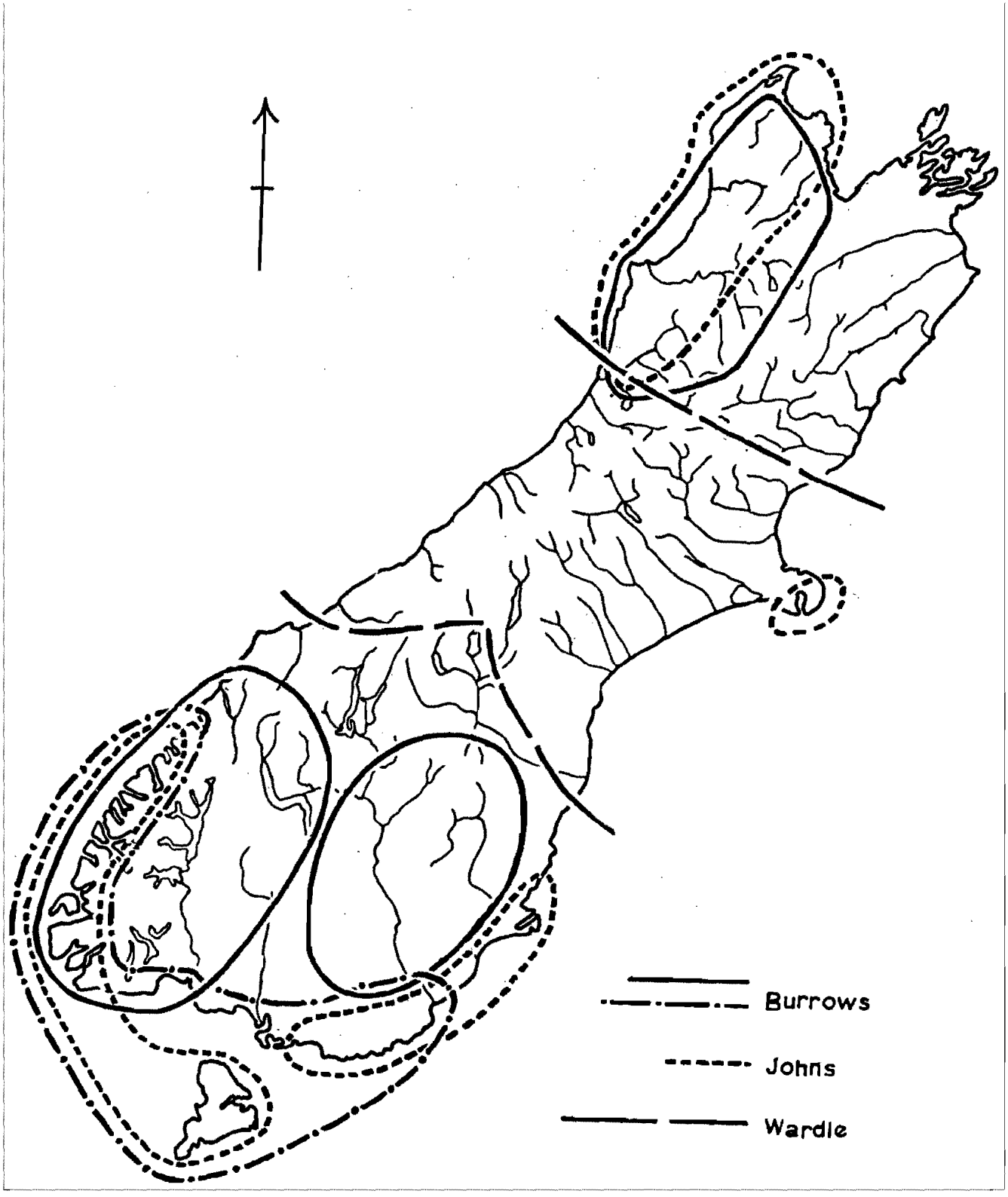
Dumbleton (1963a) suggested that the parent species of N. campbelli might be N. tonnoiri. However, as the larva of N. campbelli is more similar to N. hudsoni larva than to any other New Zealand blepharocerid and as the only known examples of brachypterous wings in the Blepharoceridae occur in these two species, it appears more probable that the parent species was N. hudsoni and not N. tonnoiri.

Neocurupira campbelli in particular, and some of the "southern" blepharocerid forms possess shortened labial palpi. This could indicate some relationship, but short labial palpi have arisen many times within the Blepharoceridae and cannot be used to indicate phylogenetic relationships. Dumbleton (1963a) believed that the short labial palpi of N. campbelli are of very recent origin as they do not fill the pupal sheath. This also applies to the labial palpi

of the "southern" blepharocerids.

If the original New Zealand blepharocerid stock possessed holoptic eyed males then it would appear that dichoptic eyed males have arisen three times within the New Zealand *Neocurupira*; in *N. tonnoiri* and *N. chiltoni*, in Forms B and D of the *hudsoni*-complex and in *N. campbelli* (Fig. 62).

A similar course of evolution is suggested by Stuckenberg (1955) as having taken place in the genus *Elporia*.


Burrows
Johns
Wardle

Refugia: The present distribution of certain groups of plants has suggested to Wardle (1963) and to Burrows (1965) that there ~~was~~ were refugia for plants during the Last Pleistocene Glaciation, in the Nelson region and in the Otago-Southland region as indicated in Figure 63.

The distribution of New Zealand terrestrial invertebrates also indicates that refugia were present, though not necessarily during during the Last Glaciation. According to R.S.Bigelow (pers.comm.) the relationships and distribution of the South Island Grasshoppers agree generally with the limits of the refugia as set by Wardle and Burrows. From the relationships and distributions of certain members of the Carabidae (Coleoptera) and Sphaerotrichoptidae (Diplopoda), P.M.Johns (pers. comm.) believes that refugia were located as shown in Figure 63.

The climatic factors, which are likely to affect the distribution of flora and terrestrial fauna during periods of glaciation, with the exception of lack of water, would probably not greatly effect the distribution of blepharocerids. Gage (1964) considered that the Last Glaciation was not as severe as has generally been believed, and that there were considerable amounts of running water present. These conditions would no doubt favour the survival and distribution of blepharocerids.

It is strange therefore that the present distribution of some of the South Island blepharocerids agree very closely with the refugia suggested by Wardle (1963), Burrows (1965) and P.M.Johns (pers. comm.). This distribution of P. turrifer within the South Island is, with the exception of the single location at Kaikoura, very similar to the refugium suggested by Burrows (1965) and P.M.Johns (pers. comm.) in North-West Nelson. The overall distribution of P. turrifer in the South Island agrees with the refugium suggested by Wardle (1963). The distribution of N. tonnoiri, though extending well down the West Coast, agrees closely with the north-western Nelson refugium suggested by Burrows and P.M.Johns (pers. comm.). Both P. turrifer and N. tonnoiri, while occurring

in open streams, are mainly found in bush covered streams, suggesting that their present distribution is in some way connected with vegetation.

The known distribution of N. campbelli and N. hudsoni fit generally the distribution of certain alpine plants which Burrows (1965) suggests survived the last Glaciation.

It is considered that Forms B and D of the hudsoni-complex may have evolved in the two southern refugia suggested by Burrows (1965) and P.M.Johns (pers. comm.).

The area of distribution of N. chiltoni agrees in general with a refugium suggested by P.M.Johns (pers.comm.) on the eastern side of Banks Peninsula (Fig. 63). However, the restricted distribution on Banks Peninsula of N. chiltoni is probably due more to lack of suitable streams on the western slopes of the peninsula than to the existence of any refugium.

To explain more fully the present distribution of New Zealand blepharocerids and in particular that of the interesting hudsoni-complex, a more detailed study of the affinities and distribution of New Zealand blepharocerids and associated freshwater fauna is required.

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CHAPTER II

THE EGGS AND EMBRYOLOGY OF SOME NEW ZEALAND BLEPHAROCERIDAE (DIPTERA, NEMATOCERA) WITH REFERENCE TO THE EMBRYOLOGY OF OTHER NEMATOCERA.

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THE EGGS AND EMBRYOLOGY OF SOME NEW ZEALAND BLEPHAROCERIDAE (DIPTERA, NEMATOCERA) WITH REFERENCE TO THE EMBRYOLOGY OF OTHER NEMATOCERA.

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Abstract

The eggs of Neocurupira campbelli, N.chiltoni, N.hudsoni and N.tonnoiri are figured and described. An egg of Edwardsina australiensis is figured.

The embryonic development of N.chiltoni and less fully, some of that of N.campbelli, is traced and the following are described: early development; the formation of germ band, nervous system, mouthparts, gut, body appendages; segmentation; blastokinesis; late embryonic development; eclosion; and rates of embryonic development.

Comparisons are made between the embryology of N.chiltoni and N.campbelli and that of certain Chironomidae, Culicidae and

Simuliidae. It is concluded that the similarities existing between the embryology of the simuliids and blepharocerids may indicate phylogenetic affinities.

INTRODUCTION

In the Nematocera a considerable amount of detailed embryological research has been carried out on the Chironomidae, Culicidae and Simuliidae. However, the accounts of Blepharoceridae eggs and embryology are fragmentary. Campbell (1921) described the oviposition and prehatching stages of N. chiltoni (Campbell). Tillyard (1922) and Tonnoir (1923) mentioned the oviposition of E. australiensis Tillyard and provided a description of the eggs, Tonnoir recorded the time of segmentation in the embryo. Mannheims (1935) described eggs, oviposition and some of the early developmental changes in the eggs of Liponeura spp. Recently, Alexander (1963) has reviewed the observations of Campbell and of Mannheims; and Giudicelli (1964) has described the oviposition of Apistomyia elegans Bigot and Liponeura bischoffi Edwards.

MATERIAL: The majority of N. chiltoni eggs used in this study were collected from the field, the remainder being obtained from laboratory reared adults. Other New Zealand blepharocerid eggs described in this paper were collected from the field. Eggs of E. australiensis were loaned by the Entomology Division, D.S.I.R., Nelson.

METHODS: Developing eggs were kept in small Petri dishes lined with damp filter paper, or in small water-filled vials. Various fixatives were tried: Bouin's fluid hot and cold tended to distort the eggs; but Carnoy's fluid was found to give adequate fixation of unpunctured eggs within 5-10 minutes. Eggs fixed for this period of time were stored without deterioration in 70% alcohol. Telford (1957) experienced difficulty with Bouin's Fluid though Gambrell (1933) and Geyer-Duszyńska (1956) used this fixative with success.

The chorion of mature eggs is tough and resilient, so that it requires softening or removal before sections can be cut. The method of De Coursey and Webster (1952) for the removal of the hard chorion of Aedes eggs with aqua regia was too violent and tended to distort blepharocerid eggs. A modification of the sodium hypochlorite method (Mortenson, 1950) was finally used and the fixed eggs were immersed for twenty-four hours in a 3% calcium hypochlorite solution at approximately 20°C. This treatment softened and sufficiently dissolved the chorion to enable sections to be cut, or for it to be removed with fine forceps.

Eggs for sectioning were orientated on small meat cubes with Mayer's Albumen, the albumen then being hardened by a short immersion in absolute alcohol. The preparation was embedded using Peterfi's Double Embedding Technique. Sections were cut at 4-6 μ and stained with Delafield's Haematoxylin and alcoholic Eosin.

Telford used Mayer's Carmalum to obtain fine surface detail of Aedes egg whole mounts; however, excellent surface details of

N. chiltoni embryos were obtained with Chlorazol Black E.

OBSERVATIONS

THE EGG: The eggs of known New Zealand Blepharoceridae are roughly para-ellipsoid in shape, with a slight flattening of the chorion on the ultimate ventral surface which is attached firmly to the substrate. The microsculpture of the dorsal or upper surface of the chorion is granulous, the raised portions being darker than the intervening portions of the chorion. The ventral surface of the chorion shows no microsculpturing at X100 magnifications. According to Giudicelli the chorion of the eggs of A. elegans and L. bischoffi eggs is completely smooth.

At X1200 magnifications the chorions in N. chiltoni and N. campbelli appear to consist of three distinct layers overlaid by a clear, substance, 51-64μ thick, which probably represents a cement layer similar to that described by Gambrell on Simulium pictipes eggs. The exochorion consists of a light brown layer 64-99μ thick, with the raised portions of the microsculpture protruding from the outer surface into the clear cement-like layer; the endochorion is 26μ thick and is heavily pigmented, accounting for the greater part of the colour of the chorion. The innermost layer is a strongly eosinophilic serosal cuticle, 32μ thick.

The micropyle, at the anterior end of the dorsal surface of

the chorion, usually consists of a rosette of dark spots arranged a r ound a central dark region, the surrounding areas being lighter in colour than the rest of the chorion (Fig. 1b).

The following descriptions of eggs are based on fresh material; the remarks concerning colour refer only to the dorsal or upper surface of the chorion.

Neocurupira campbelli Dumbleton (Fig. 1a).

Size: 0.65 x 0.25 mm. Very heavily granulous, almost black in colour. Micropyle not in rosette form, but a dense black structure with a small clear central region.

Neocurupira chiltoni (Campbell) (Fig. 1b).

Size: 0.68 x 0.24 mm. Ends more rounded than other eggs. Lighter in colour than N. campbelli but darker than N. hudsoni. Without dark spots at ends of rosette arms as in N. hudsoni.

Neocurupira hudsoni Lamb (Fig. 1c).

Size: 0.70 x 0.25 mm. Ends more tapered than in other species of Neocurupira and lighter in colour. Micropyle in rosette form with dark spots at ends of rosette arms.

Neocurupira tonnoiri Dumbleton (Fig. 1d).

Size: 0.62 x 0.22 mm. Apart from smaller size, difficult to distinguish from eggs of N. chiltoni.

Mature eggs of Peritheates spp. were not available but eggs dissected from adults and pharate adults of this genus are very similar in shape to those of Neocurupira though smaller in size:

Peritheates harrisi (Campbell).

Size: 0.58 x 0.28 mm.

Peritheates intermedius Tillyard.

Size: 0.52 x 0.16 mm.

Peritheates turrifer Lamb

Size: 0.59 x 0.19 mm.

The shape of New Zealand blepharocerid eggs is similar to that described and figured for Apistomyia elegans and Liponeura bischoffi by Guidicelli and for L. cinerascens Loew by Mannheims. The eggs of the primitive Australian blepharocerid Edwardsina australiensis are more flattened dorsoventrally and pointed apically than the eggs of New Zealand blepharocerids (Fig. 1e).

EARLY DEVELOPMENT AND GERM BAND FORMATION: As the living embryo is transparent and shows no surface detail until approximately the 22nd day, the following description is based on fixed material. The ages of embryos quoted refer to development at 12°C.

When newly laid, the eggs of N. campbelli and N. chiltoni are creamy-white in colour, but turn bluish and then brown-black on the dorsal surface of the chorion within 3-4 hours. The dark central region of the micropyle appears immediately after oviposition and at the same time the oosome (Johannsen and Butt, 1941) appears at the posterior end of the egg.

Alexander and Mannheims each described similar changes for other blepharocerid eggs. Mannheims considered the darkening of the

chorion to be due to chemicals in the water, however, Giudicelli states that the process of melanisation of the chorion is due to the action of a tyrosinase on breakdown products of protein.

Attempts to detect early stages of development, such as maturation division and formation of the blastoderm, were not successful.

Sections of newly laid eggs of N. chiltoni show the presence of an extremely thin vitelline membrane and sections of 24-hour eggs of N. campbelli and N. chiltoni show the blastoderm to be spread evenly over the yolk. By the 4th day the embryonic membranes are formed and the germ band appears as a bilobed structure on the ventral surface of the yolk, showing the gastrular groove and the sero-amniotic opening (Fig. 2a). The amnion of N. campbelli and N. chiltoni is composed of extremely flattened cells with prominent nuclei while the serosa is made up of thicker cells (Fig. 4).

The germ band, prior to blastokinesis, is directed away from the substrate, but nevertheless defines the ventral surface of the yolk. As the germ band commences to elongate, on approximately the 6th day, yolk shrinkage occurs. This appears to be associated with the growth of the tail region of the germ band posteriorly and then dorsally over the yolk. By the end of the 6th day, the head lobe has curved over onto the anterior end of the yolk (Figs. 2b and 3a). Longitudinal shrinkage of the yolk in N. chiltoni continues until the 9th day, by which time the tail region of the

embryo has progressed along the dorsal surface of the yolk and now almost underlies the head lobe (Fig. 3b). In comparison the tail region and head lobe of N. campbelli are very closely applied during this stage.

Often in 8-day eggs of N. chiltoni the elongated germ band buckles laterally and describes a curved path across the yolk (Fig. 2b).

SEGMENTATION: Sections of 7-day eggs of N.chiltoni show that the mesoderm of the germ band becomes segmented before the ectoderm. Segmentation on the surface of the germ band of N. chiltoni is visible at approximately the 8th day. Tonnoir (1923) states that the segmentation of Edwardsina australiensis was visible in fresh eggs after nineteen hours (temperature of incubation not given). A sample of E. australiensis eggs was available from Tonnoir's collection, but sections unfortunately showed no signs of segmentation.

By early 9th day the antennal, mandibular, maxillary and labial segments are clearly defined. Lying between the antennal and mandibular segments are two triangular intercalary segments (Johannsen and Butt) (Figs. 2c and 3b). These intercalary segments are resorbed by the eleventh day. Segmentation progresses from the anterior to the posterior in a fashion similar to that described by De Coursey and Webster, and Rosay, so that by the 10th day a total of seventeen segments is apparent (Fig. 3c). The antennal and three gnathal segments are followed by three thoracic and ten abdominal

segments.

There has been considerable disagreement concerning the number and arrangement of the segments of larval blepharocerids, due to the amount of fusion in the anterior and posterior segments. The main differences in interpretation centre around the number of abdominal segments fused into the cephalic and anal divisions, and the relation of the suckers to these segments. Some of the interpretations by various authors are presented in chronological order in Table 1.

Further development of the embryos of N. campbelli and N. chiltoni shows that only the first abdominal segment fuses with the thorax and head to form the cephalic division and that there are four fused abdominal segments in the anal division. This is in complete agreement with Mannheim's interpretation.

FORMATION OF THE NERVOUS SYSTEM: Before the intercalary segments are resorbed on the eleventh day, a deep neural groove is formed (Fig. 2c). This extends from the stomodaeum to the last abdominal segment. External evidence of neurulation is obliterated by the thirteenth day (Fig. 2d) and sections at this stage show that each thoracic and abdominal segment has already a definite ganglion.

As the thoracic segments regress, the individual thoracic ganglia are observable through the thin ectoderm (Figs. 2f, 2h, 5 and 8). As external evidence of the thorax becomes obliterated by the anterior movement of the developing first abdominal sucker, the sub-oesophageal and the first thoracic ganglia become closely

applied but retain their individual nature. However, the second and third thoracic ganglia plus the first abdominal ganglion become fused into a single structure. The original constituents of the fused ganglion can be clearly identified in longitudinal sections. The identity of the first abdominal ganglion is further suggested by the first abdominal sucker apparently retaining its innervation from this ganglion (Fig. 9).

The regression and fusion of the 7th-10th abdominal segments is such that by the eighteenth day the ganglia protrude beyond the remainder of the abdominal ectoderm (Figs. 2f, 3f and 6). The ganglia of the 7th-10th segments then completely fuse into a single posterior ganglion and there is then no longer any indication of the individual ganglia in longitudinal sections.

Mannheims investigated the structure of the ganglion in the cephalic division of larval blepharocerids but failed to determine the relationship of the fused thoracic and first abdominal ganglia. He pointed out that such an investigation would be better carried out on embryonic blepharocerids.

MOUTHPART FORMATION: The mandibular rudiment, though large initially, regresses and becomes comparatively small as the development of the maxilla proceeds (Figs. 2d, 2h and 2i). The maxillary rudiment constricts into two portions, distal and basal (Figs. 2d and 3d). The distal portion eventually forms the maxillary palp, which grows dorsally then posteriorly and later covers the lateral

margin of the labial rudiment and a small part of the first thoracic segment (Figs. 3d and 3e). The posterior part of the maxillary palp grows medially at the same time as the two labial rudiments fuse into a single median structure (Figs. 2d, 2e and 2f). The basal portion of the maxillary rudiment grows anteriorly forming a curved plate which covers the mandibles laterally and medially (Figs. 2h, 2i, 2j, 3f and 3g). This plate forms the galea and the lacinia. The labrum arises as a single lobe anterior to the stomodaeum and by the eleventh day is bilobed, becoming single lobed again by the thirteenth day.

Bischoff (1928) interpreted the structure formed from the distal lobe-like portion of the maxillary rudiment as the "Mentallappen (Polster)" and the median sensory structure on the maxilla as the maxillary palp. Craig (———) on the basis of comparative embryology with other insect orders, and with evidence from the musculature of the larval maxilla, shows that the distal lobe is probably the true maxillary palp and the median sensory structure the lacinia.

BLASTOKINESIS: Blastokinesis or the rotation of the yolk and embryo through 180°, occurs in N. chiltoni on approximately the eleventh day, normally taking only a few hours but in some cases requiring up to two days to complete. The ventral surface of the embryo is then directed towards the substrate. (Figs. 3d, 3e, 3f and 3g are presented in the pre-blastokinesis orientation for clarity.)

Associated with blastokinesis of N. chiltoni is the shrinkage of the tail region which until now has lain along the dorsal surface of the yolk. By the fourteenth day the tail region lies almost completely on the ventral surface (Fig. 3d).

At the same time as blastokinesis occurs in N. chiltoni the embryo begins to swell, completely filling the chorion by the twenty-second day. Considerable pressure appears to be exerted on the chorion as the egg changes shape slightly and the initial hatching movement is violent.

GUT FORMATION: Stomodaeum formation takes place with the advent of segmentation and first appears as an anterior invagination of the germ band on the seventh day. Development of the proctodaeum does not begin until the tail region of the embryo shortens on approximately the fourteenth day. However, development of the proctodaeum is rapid and by the twentieth day it has assumed the simple coiled shape of the hind gut of larval blepharocerids described by Müller (1879). By the twentieth day the stomodaeum and the proctodaeum intrude into the yolk, but there is little evidence yet of midgut formation, although by this stage the yolk is becoming enclosed with the body wall (Fig. 3g). By the twenty-eighth day the midgut epithelial rudiment has enclosed the yolk completely (Fig. 9).

BODY APPENDAGES: The thoracic appendages develop on the fourteenth day as medially directed lobes on the posterior margin of the thoracic

segments. The line of the thoracic prolegs is continued onto the abdominal segments as a faintly visible abdominal ridge (Fig. 2d). By the sixteenth day the thoracic prolegs have become peg-like (Fig. 2e), and begin to move anteriorly as the embryo elongates and as the thoracic segments are compressed by the enlarging abdominal segments (Fig. 2f). By the twenty-second day the prolegs have completely regressed. Fusion of the thoracic segments is completed by the twenty-second day, but their regression continues until the twenty-eighth day by which time the developing first abdominal sucker has moved anteriorly (Figs. 2h, 2i and 2j) and lies ventral to the first and second thoracic ganglia (Fig. 9).

Development of the suckers begins on approximately the twentieth day, as the ventral ectoderm of the first to sixth abdominal segments becomes thickened and raised into median blocks (Fig. 2g). By the twenty-fourth day the pistons of the suckers show as distinct central regions on the raised blocks of ectoderm (Fig. 2h). Sections at this stage show that the piston already has muscle attachments and is surrounded by a cylinder of ectoderm (Fig. 7), which develops into the fleshy rim of the sucker (Fig. 9). Bischoff, Hora (1930) and Komáreck (1914) give detailed accounts of the fully developed blepharocerid sucker.

The abdominal prolegs (pseudopods, Johannsen) of the first six abdominal segments begin development on the twentieth day (Fig. 2g) as low projections from the abdominal ridge, which lies in series with the now almost regressed thoracic prolegs. The method of

development and the histological similarities (Fig. 5 and 7) between the thoracic and the abdominal prolegs suggest that they are homologous structures. The large lobes of ectoderm flanking the protruding ganglia of the seventh to the tenth abdominal segments (Figs. 2f and 3f) show serial and histological similarities (Figs. 2f, 2g, 5, 6 and 7) to the thoracic prolegs and to the prolegs of the first six abdominal segments. This suggests that they may represent the rudimentary prolegs of the seventh to tenth abdominal segments.

The prolegs of the first six abdominal segments become cone-shaped and by the thirty-second day (Fig. 2j) have developed the extensile tip described by Tonnoir (1924) as typical of first instar larvae of blepharocerids. The ectodermal lobes of the seventh to tenth abdominal segments regress and fuse into the anal division.

LATE EMBRYONIC DEVELOPMENT: The anal blood gills begin development on approximately the twenty-fifth day. The two pairs are initially the same size, but the most lateral pair grows larger by the twenty-sixth day (Fig. 2i) and by the thirty-second day have moved posteriorly from the smaller anterior blood gills (Fig. 2j). By the twenty-eighth day the ocelli are visible as red structures on the antero-lateral surface of the cephalic division. The suckers become pigmented on the thirty-second day and at approximately this time the embryo becomes capable of movement. Move-

ments have been observed of mouth parts, suckers and abdominal prolegs. During the thirty-fourth day the sclerite of the egg-burster becomes heavily pigmented as do the latero-dorsal body spines, and by the thirty-seventh day all body spines are clearly visible through the chorion.

The egg-burster (egg-tooth, Wigglesworth 1964; hatching-spine, Clements 1963) of N. campbelli and N. chiltoni is a relatively long blade-like structure supported by a strong median sclerite lying between the ocelli. The supporting sclerite is sunken into the surrounding cuticle so that the sharp edge of the egg-burster is just below the lip of the groove. The blade-like egg-burster of the blepharocerids is probably forced against the chorion of the egg by pressure of the body fluids as no protractor muscles have been detected in sections. The mouth part movements prior to eclosion may indicate manipulation of the egg-burster or perhaps active gnawing at the chorion. Egg-bursters have been reported for simuliids (Puri, 1925) and the culicids (Clements, and Wigglesworth).

ECLOSION: Eclosion takes place on the thirty-ninth to fortieth day. The chorion splits dorsally, commencing at the micropyle and progressing posteriorly, the split almost without exception curving away to the right. Giudicelli reports similar dehiscence of the chorion in eggs of Apistomyia and Liponeura. The larva is partially ejected in the violent hatching movement, suggesting a hatching mechanism of a hydraulic nature. The larva then

attaches the anterior suckers to the substrate and pulls the remainder of its body free. The newly hatched larvae of N. chiltoni range from 0.8 mm to 1.1 mm. in length. The colour of the newly hatched larva is initially creamy-white but darkens to black-brown within two to three hours.

RATES OF EMBRYONIC DEVELOPMENT: Eggs of N. chiltoni laid in the laboratory and of known age were incubated at a series of constant temperatures ranging from 0°C to 27°C. The temperature of any one experiment never varied more than ± 1.5°C from the mean temperature (Fig. 10).

Development and hatching were normal only at temperatures between 4°C and 18°C. Eggs reared at 20°C developed to full term embryos, but few hatched. Eggs incubated at 0°C failed to develop and it was found that exposure to this temperature for as little as twenty minutes was lethal. A constant temperature of 25°C was found to be lethal, however, eggs could withstand exposure to 27°C for up to five hours before failing to develop at suitable lower temperatures.

DISCUSSION: The structure of the chorion of N. campbelli and N. chiltoni is similar to that of the culicid eggs as described by Clements, who also pointed out that the exochorion and endochorion are soluble in hypochlorite solutions. Gambrell describes only two membranes on the eggs of Similium pictipes besides the cement

layer, a thin chorion and vitelline membrane. Early gastrulation and formation of the embryonic membranes similar to that occurring in the embryos of N. campbelli and N. chiltoni, are described for S. pictipes by Gambrell. However, the embryonic membranes of the culicids (Clements, 1963) and of the chironomids (Miall and Hammond 1900) are formed at a much later stage than gastrulation. The amnion and serosa of the simuliids and culicids differ from those of N. campbelli and N. chiltoni in that the amnion is composed of thick cells and the serosa of very thin cells with prominent nuclei.

The germ bands on the yolk of N. campbelli and N. chiltoni at the 8-day stage are relatively narrow structures and are at the most only slightly embedded in the yolk. The germ bands of some simuliids (Gambrell, and Mecznikow 1866) are also narrow at a comparable stage, but the tail regions are deeply embedded in the yolk. The germ bands of the culicids (Clements, Rosay 1959) and of the chironomids (Miall and Hammond) are considerably wider, the tail region of the chironomids being deeply embedded in the yolk.

At a stage comparable to that of an 8-day N. chiltoni egg, where the germ band curves laterally over the yolk, Rosay describes vertical folding in the germ band of Culex tarsalis. The faint indentations visible on the germ band of the 8-day N.chiltoni egg (Fig. 2b) are early indications of segmentation and not merely folding as in C. tarsalis.

The initiation of segmentation in the mesoderm of the germ band of N. chiltoni follows the pattern common to many Arthropods

(Johannsen and Butt; Manton 1960). However, Clements states that in the culicids the mesoderm differentiates later than the ectoderm. The association of blastokinesis and tail region shrinkage as in N. chiltoni also occurs in Culex tarsalis, but they do not appear to be associated in Simulium pictipes. The amount of rotation during blastokinesis of C. tarsalis and S. pictipes embryos is similar to that of N. chiltoni, however, Miall and Hammond state that blastokinesis in Chironomus eggs takes place in two stages through a total of 360°.

The development of the larval labrum of N. chiltoni, from a single lobe which becomes bilobed for a short period, agrees with the general labral development as put forward by Crampton (1921). Butt (1960), however, states that in many insects the labrum arises as a double structure and that the labral lobes represent the appendages of the intercalary segments, the intercalary appendages migrating around the mouth preorally and fusing to form the labrum. Manton refutes Butt's statements and points out that there is much unequivocal evidence that Butt apparently disregards. This evidence shows clearly that the labrum is not formed by the fusion of preoral appendages and is definitely not formed from the intercalary segments.

Although the thoracic and abdominal prolegs of N. chiltoni show positional and histological similarities suggesting that they are homologous (page 13 and 14), Hinton (1955) believes that the abdominal prolegs of dipterous larvae have been secondarily evolved

and he presents considerable evidence to show that they are not homologous with the thoracic prolegs. The origin of the suckers from raised ectodermal blocks on the ventral surface of the abdominal segments indicates that contrary to Hora's (1930 and 1933) theory, they did not evolve from fused paired abdominal prolegs, but rather by modification of the ventral surface of the body as suggested by Tonnoir (1933).

CONCLUSION: Apart from the differences in the chorion, embryonic membranes and in the invagination of the tail region of the germ band, the initial embryonic development of N. campbelli and N. chiltoni shows greater similarities to the published accounts of simuliid embryology than to those of the embryology of other Nematocera. This may indicate that the Blepharoceridae have closer phylogenetic affinites to the Simuliidae than to other Nematocera.

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LIST OF ABBREVIATIONS

ab 10	Abdominal segment 10
abg.	Abdominal ganglion.
abg 1.	Abdominal ganglion 1.
abp.	Abdominal proleg.
abr.	Abdominal ridge.
ag.	Anal gills.
am.	Amnion.
ant.	Antenna.
cg.	Cerebral ganglion.
ect.	Ectoderm.
gb.	Germ band.
gg.	Gastrular groove.
hl.	Head lobe.
int.	Intercalary segment.
lb.	Labium.
lr.	Labrum.
mge.	Midgut epithelium.
md.	Mandible.
mi.	Micropyle.
mx.	Maxilla.
mxp.	Maxillary palp.
ng.	Neural Groove.
p.	Piston.
pr.	Proctodaeum.
sa.	Sero-amniotic opening.
se.	Serosa.
sk.	Sucker.
st.	Stomodaeum.
subg.	Sub-oesophageal ganglion.
th1.	Thoracic segment 1.
th3.	Thoracic segment 3.
thg.	Thoracic ganglion.
thg1.	Thoracic ganglion 1.
thp.	Thoracic proleg.
Vent.	Ventral surface.
y.	Yolk.

Fig. 1 Dorsal views of Blepharocerid eggs.

1a *Neocurupira campbelli*

1b *N. chiltoni*

1c *N. hudsoni*

1d *N. tonnoiri*

1e *Edwardsina australiensis*

Fig. 2 Ventral views of developing embryos of *N. chiltoni*

2a 4-day embryo

2b 8-day "

2c 9-day "

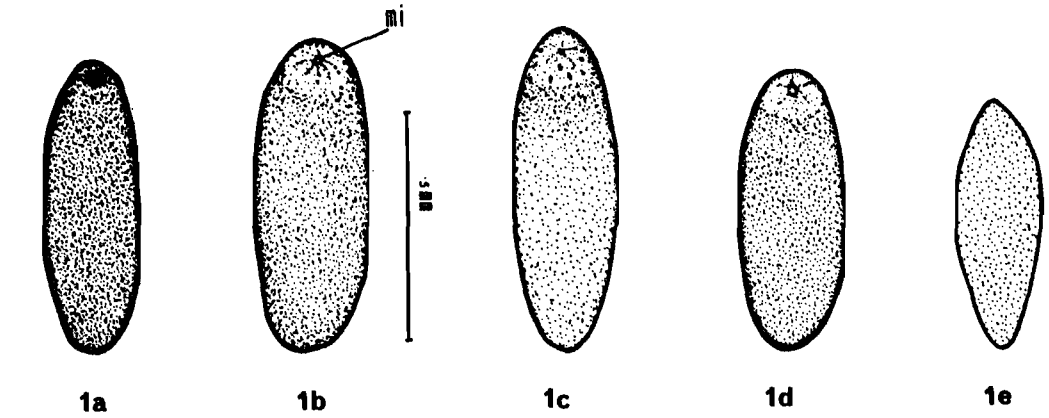
2d 14-day "

2e 16-day "

2f 18-day "

2g 20-day "

2h 24-day "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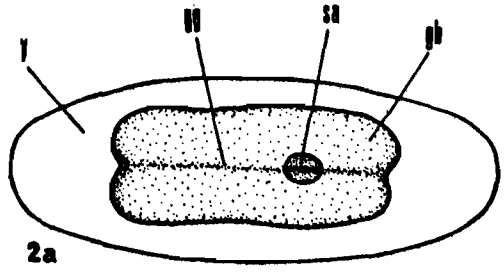
1a
1b
1c
1d
1e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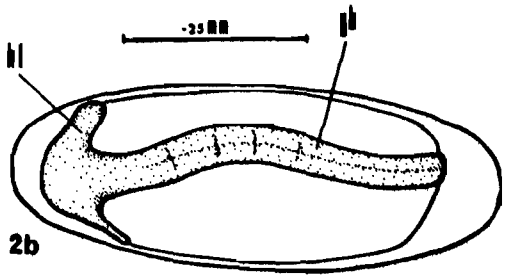
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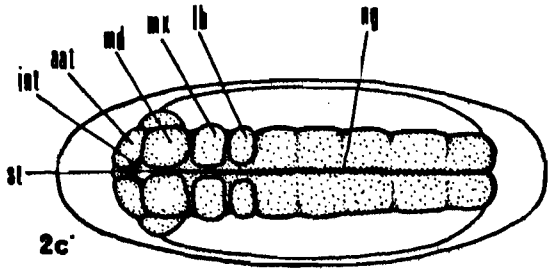
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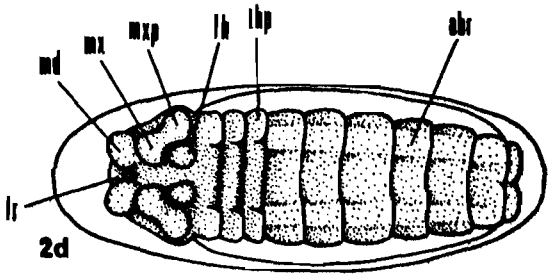
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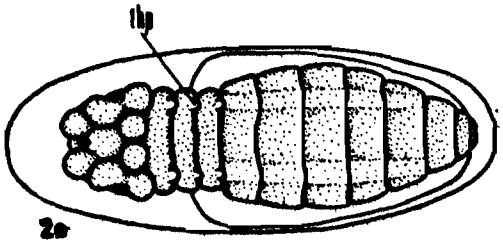
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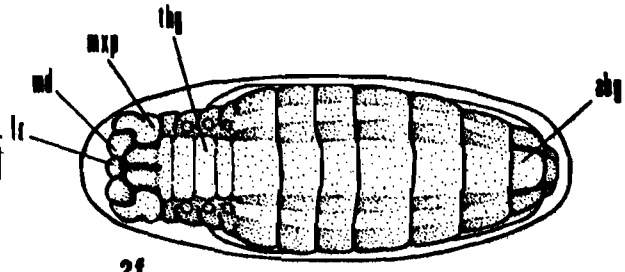
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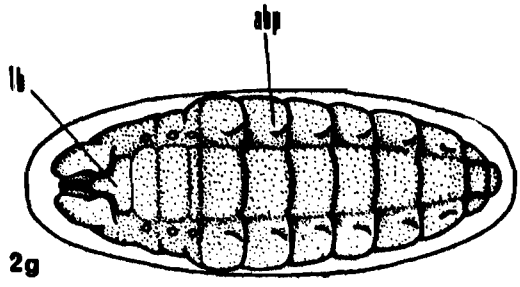
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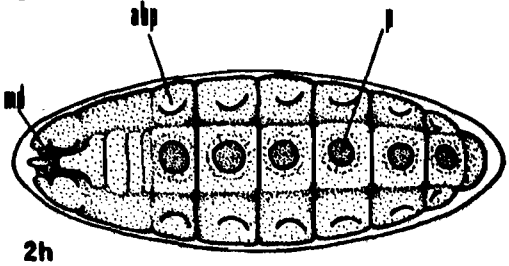
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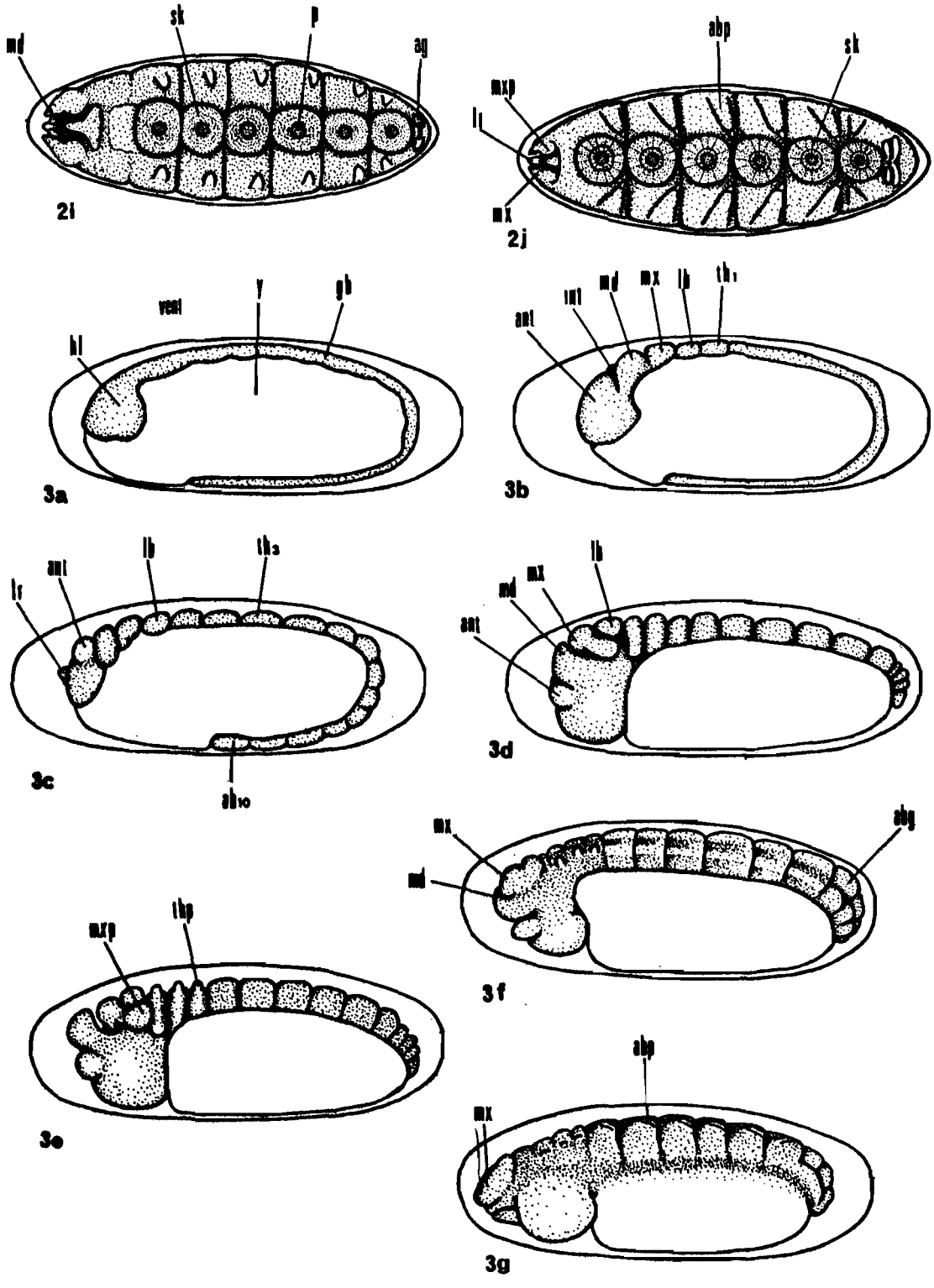
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th1
ant
3b
lr
ant
lb
th3
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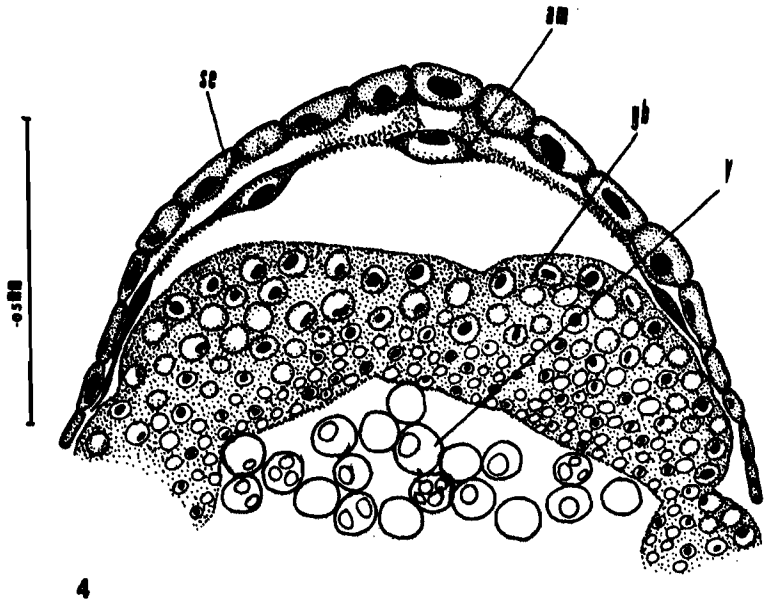

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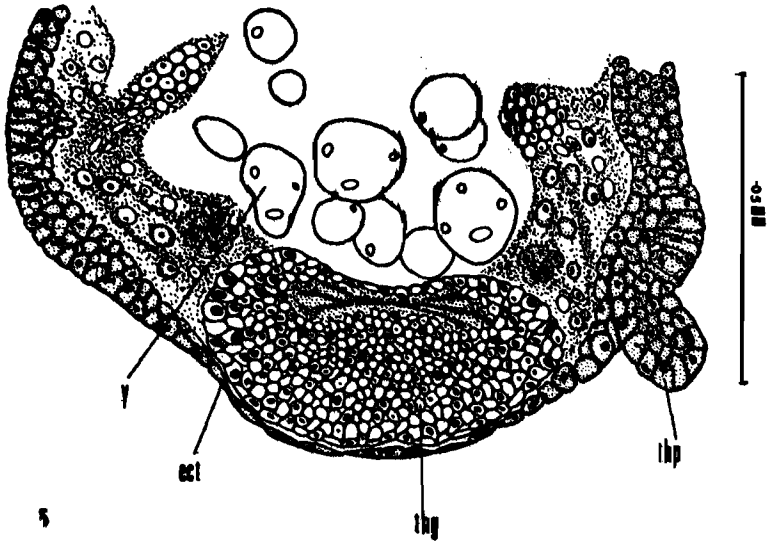

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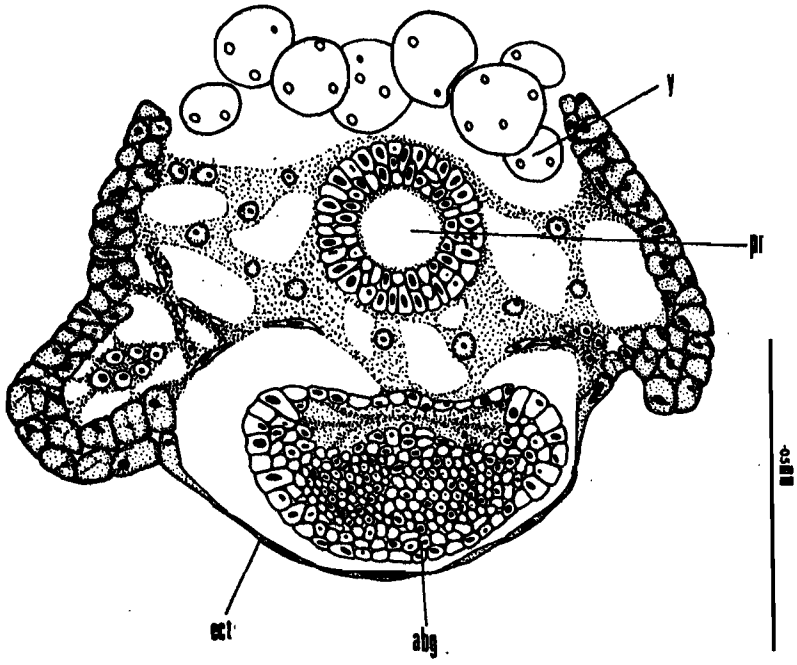

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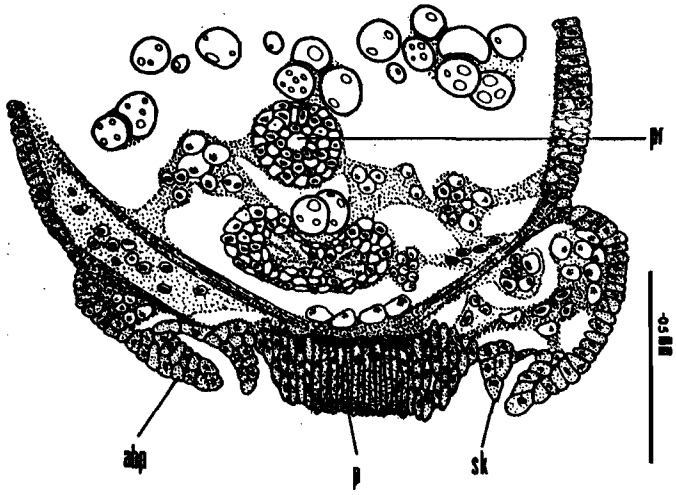
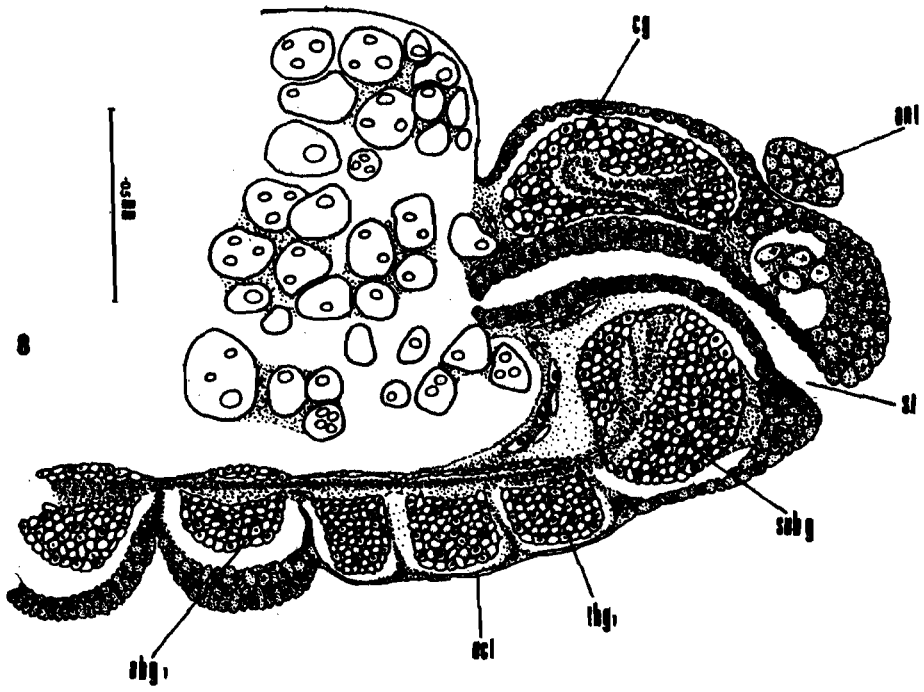


Fig. 8 L.S. of head and thorax of 25-day embryo of *N. chiltoni*.

Fig. 9 L.S. of head and thorax of 28-day embryo of *N. chiltoni*.



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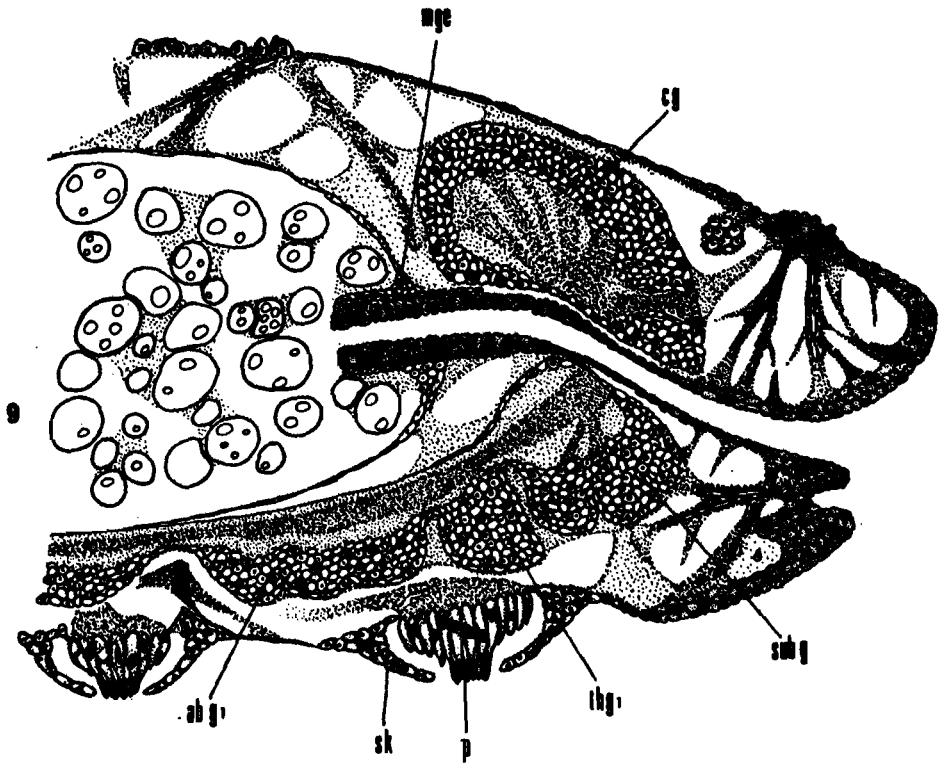

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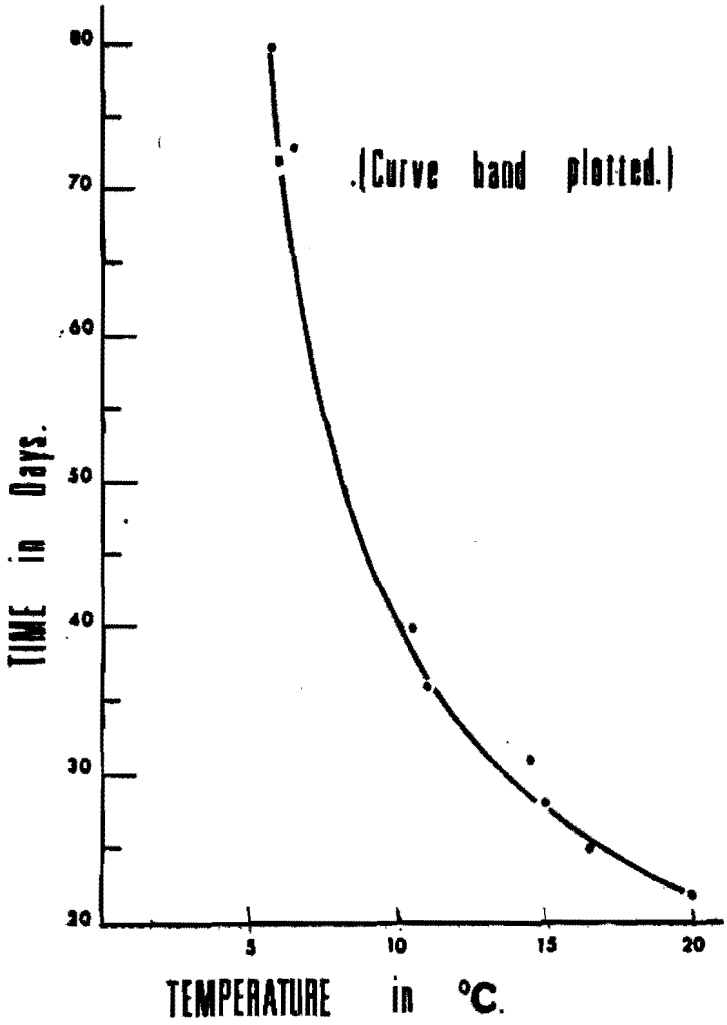

(Curve band plotted.)
80
70
60
50
40
30
20
TIME in Days.
5
10
15
20
TEMPERATURE in °C.

CHAPTER III.

THE ECOLOGY AND LIFE CYCLES OF SOME NEW ZEALAND BLEPHAROCERIDAE.

INTRODUCTION.

Various aspects of the biology of the Blepharoceridae have been discussed by Kellogg (1900 and 1903), Hetschko (1911 and 1912), Bischoff (1928), Mannheims (1935), Wesenberg-Lund (1943), Kitakami (1950), Alexander (1963) and Dumblelton (1963a). Of these Mannheims, Bischoff and perhaps Kitakami have given the most comprehensive accounts.

To investigate the biology of some N.Z. blepharocerids, samples were taken at regular intervals from blepharocerid populations at Purau Stream, Kaituna River and Bealey River. The Purau and Kaituna populations containing only Neocurupira chiltoni, were chosen because of their proximity to Christchurch. The Bealey Chasm population was chosen to compare with those of Purau and Kaituna because of its variety of blepharocerid species and differing climatic conditions.

As well as the study areas three other blepharocerid habitats are described.

In addition to regular samples of blepharocerids, samples of the larval and adult associates were taken.

Records were kept of Maximum and Minimum air and water temperatures, of water level, of pH, and whenever possible of the % O_2 saturation and of the concentration of dissolved substances in the water.

a

b

PLATE 1.

Upper portion of the Purau Stream study area, showing lower end of pool and rapid area.
(a). 14-iv-63. Typical winter water level.

(b). 4-i-64. Approximately same view as (a), the effects of the 21st December, 1963 flood are obvious. Summer water level.

PART I. DESCRIPTION OF HABITATS.

Purau Stream.

This stream is located in Purau Valley, Banks Peninsula, 21 miles from Christchurch. The Peninsula is a remnant volcanic cone last active during the Holocene (Liggett and Gregg 1965), and Purau Valley has been eroded from Pliocene lava of the Lyttelton Group consisting of basalt, andesite and trachyte. Purau Stream, spring fed, arises at 2550 ft. and drains the north-eastern slopes of Herbert Peak (3015 ft.). The stream is approximately 4 miles long. It descends 1800ft.in the first two miles and 250ft.in the third mile, before flowing gently through flat farm land and emptying into Lyttelton Harbour.

Remnants of the original bush cover are found along the sides of the stream and consist mainly of Asplenium sp., Carpodetus serratus, Coprosma sp., Leptospermum sp., Polystichum sp., Sophora tetraptera and Urtica ferox.

The upper slopes of the valley above the bush are covered by the native tussocks Poa caespitosa, Festuca novae-zelandica and Danthonia pilosa.

Study Area (Plate 1): The study area, (N.Z.M.S.I.SHEET 84 105411), approximately 3/4 of a mile from the mouth of the stream, was at an altitude of 250 ft. It consisted of a section of the stream approximately 60 m. long with a pool at the upstream end, then a short rapid with a gradient of 7 degrees, and finally a moderately swift portion with a gradient of 5 degrees. (Gradients were measured with an Abney level). The area was modified by flooding on the 21st December 1963 (p.12), when the short rapid section was deeply scoured and cut back into the upper pool. (cf Plate 1a & b). The stream at this point has a catchment area of 5.5 square miles (measured from a map of the catchment area). The width of the stream in the study area varies from 1-3 m. and the depth from 8-30 cm.

The proportions of the differently sized rocks and their arrangement varies greatly within the study area. While testing sampling techniques in an area of 3sq.m., at the upstream end of the rapid, the following rocks were found:-

(size given as greatest transverse measurement).

Size.	Number.	Weight.	Condition.
31-90 cm.	10	10-> 10 Kg	Embedded.
15-30 cm.	24	1-2 Kg	Free.
5-8 cm.	Remainder	<1 Kg	Free.

There were no rocks with weights between 2-10 Kg and there was little sand or fine gravel between rocks. The bottom of the pool at the upper end of the study area was composed of rocks 15-30 cm. in size with a 1-2 cm. deep covering of fine silt.

Even though the embedded rocks are stable, flooding has caused considerable scouring to the stream bed.

Whenever possible the Purau study area was sampled at fortnightly intervals.

Kaituna River.

This river is located in Kaituna Valley, 34 miles from Christchurch and is also on Banks Peninsula. The valley is south of Purau Valley. Kaituna River , probably spring fed, arises at approximately 2400 ft. and drains the southern slopes of Mount Herbert (2805 ft.), Herbert Peak and the western slopes of the ridge that separates Kaituna Valley from Western Valley, Little River. The stream is approximately 8.5 miles long and descends 1300 ft. in the first mile, 600 ft. in the second mile and 250 ft. in the next mile and a quarter. For the remainder of the distance it flows sluggishly through flat fertile farm land finally emptying into Lake Ellesmere.

The valley, like Purau Valley, has been eroded out of Lyttelton Group lava.

Remnants of the original bush cover are more plentiful than in Purau Valley, with bush covering parts of the southern slopes of Mount Herbert. The bush and tussock grasses are similar to those at Purau.

Study Area: The study area, (N.Z.M.S.I. SHEET 84 068334), approximately 6.5 miles upstream from the Christchurch-Akaroa Highway, is at an altitude of 700 ft. It consists of a section of stream approximately 40 m. long with a cascade dropping 2 m. at the upstream end. The remainder of the area is a series of smaller cascades separated by quieter stretches. The overall gradient from below the upper cascade is approximately 4 degrees. The stream at this point has a catchment area of 2.3 sq. mls.

The width of the stream in the study area varies from 0.3-2 m. and the depth from 12 cm. - 30 cm.

The bed rocks are volcanic, but are more uniform in size than at Purau. The majority of the rocks are over 30 cm. in size and are embedded. There is a lack of rocks from 15-30 cm. in size. The spaces between the larger rocks are filled with stones 5-14 cm. in size.

The runoff is slower at Kaituna than at Purau because of the greater bush coverage of the catchment area. This, coupled with the more stable stream bed, produces less flood-scouring than at Purau.

The Kaituna River study area was sampled at approximately fortnightly intervals from August 1964 after a flood again scoured the bed of Purau Stream.

a

b

PLATE 2.

Views of the study area at Bealey Chasm.

(a). 21-iii-64. Water level approximately 2.5 ft. above datum line. Flood Conditions.

(b). 18-v-66. View slightly to the right and lower than that of (a). Water level approximately 2 ft below datum line.

The arrows indicate the same rocks in each photograph.

Bealey River.

The Bealey River is located in the Arthur's Pass region, 95 miles from Christchurch. The river which is over 8 miles long is largely snow fed and arises at approximately 5700 ft. The upper reaches of the river drain the eastern slopes of Mount Rolleston (7453 ft.) and western slopes of Phipps Peak (6700 ft.), Mount Temple B'Limit (6650 ft.) and Mount Cassidy (5750 ft.). It descends 3200 ft. in the first two miles in a series of waterfalls and rapids, but only 250 ft. in the next 1.25 miles before flowing onto a wide alluvial river bed and emptying into the Waimakariri River.

The valley slopes are heavily bushed up to nearly 4500 ft. Above this the bush gives way to subalpine scrub and then tussock grassland and scree. The main plant species on the banks of the study area are:-

Trees. Olearia sp., Nothofagus cliffortioides, Nothopanax colensoi.
Shrubs. Archeria sp., Coprosma spp., Coriaria angustissima, Dracophyllum sp., Hebe spp., Phormium colensoi.
Herbs. Angelica sp., Cotula sp., Anisotome sp., Acaena sp.
Ferns. Blechnum capense, Polystichum vestitum.

Study area. (Plate 2): The study area (N.Z.M.S.I. SHEET 59 050313), for convenience called Bealey Chasm, is approximately 2 miles from Arthur's Pass Township, and is located just above Bealey Chasm proper at an altitude of 2750 ft. It consists of a stretch of river approximately 50 m. long, with the upstream limit at an approximately 1 m. high cascade. The study area consists mainly of rapidly flowing channels of water interrupted by embedded boulders. The downstream limit is at the bridge crossing Bealey Chasm proper, into which Bealey River plunges over a 3 m. high waterfall. The overall gradient of the study area is 5 degrees. The river at this location has a catchment area of 3.5 sq. mls.

PLATE 3.

View of Coads Creek, Nelson. Waterfall above walking track.

The bed is composed mainly of Greywacke and Argillite in the form of small boulders 0.6-1.5 m. in size which produce small cascades. A few larger boulders 1.5-2.0 m. in size, channel the water into rapidly flowing streams. Gravel and sand are only present in very sheltered places.

From December 1962 collections were made here at monthly intervals whenever possible, but the terrain and winter conditions, at times, made this extremely difficult.

Other Habitats. The following are some rather unusual blepharocerid habitats sampled during the course of this study: -

Tributary to Pu-Pu Spring River: Located 3.5 miles from Takaka (N.Z.M.S.I. SHEET S8 171822), this river bed consists of white quartz stones 12-30 cm. in size which are embedded or firmly implanted in a fine gravel substrate. The river varied in width from 10-12 m. and in depth from 36-60 cm. Thus, there were no protruding stones. The water was smoothly flowing with a velocity of approximately 180 cm. per sec.

The larger rocks were partially covered with a brown encrusting alga and various hepatics. Blepharocerid larvae were found only on clear spaces on these rocks. Adults were found resting on vegetation which overhung the water.

The surrounding vegetation is mainly Leptospermum ericoides, Ulex europaeus and Blechnum minor.

Coads Creek. (Plate 3): Located approximately 7 miles east of Nelson at an altitude of 2700 ft. (N.Z.M.S.I. SHEET S20 687205), this stream bed consists of large pieces of bedrock with few free rocks of any size. The stream is 30-60 cm. wide and 4-6 cm. in depth and consists of a series of small waterfalls and pools. The stream is heavily overhung with mixed bush and scrub and the rocks bear luxurious growths of algae and hepatics especially in the hygropetric zone. Blepharocerid larvae are largely confined to the bottom of waterfalls in vegetation free areas.

Tributary to the North Opuha River: This is a snow fed stream

Fig.1

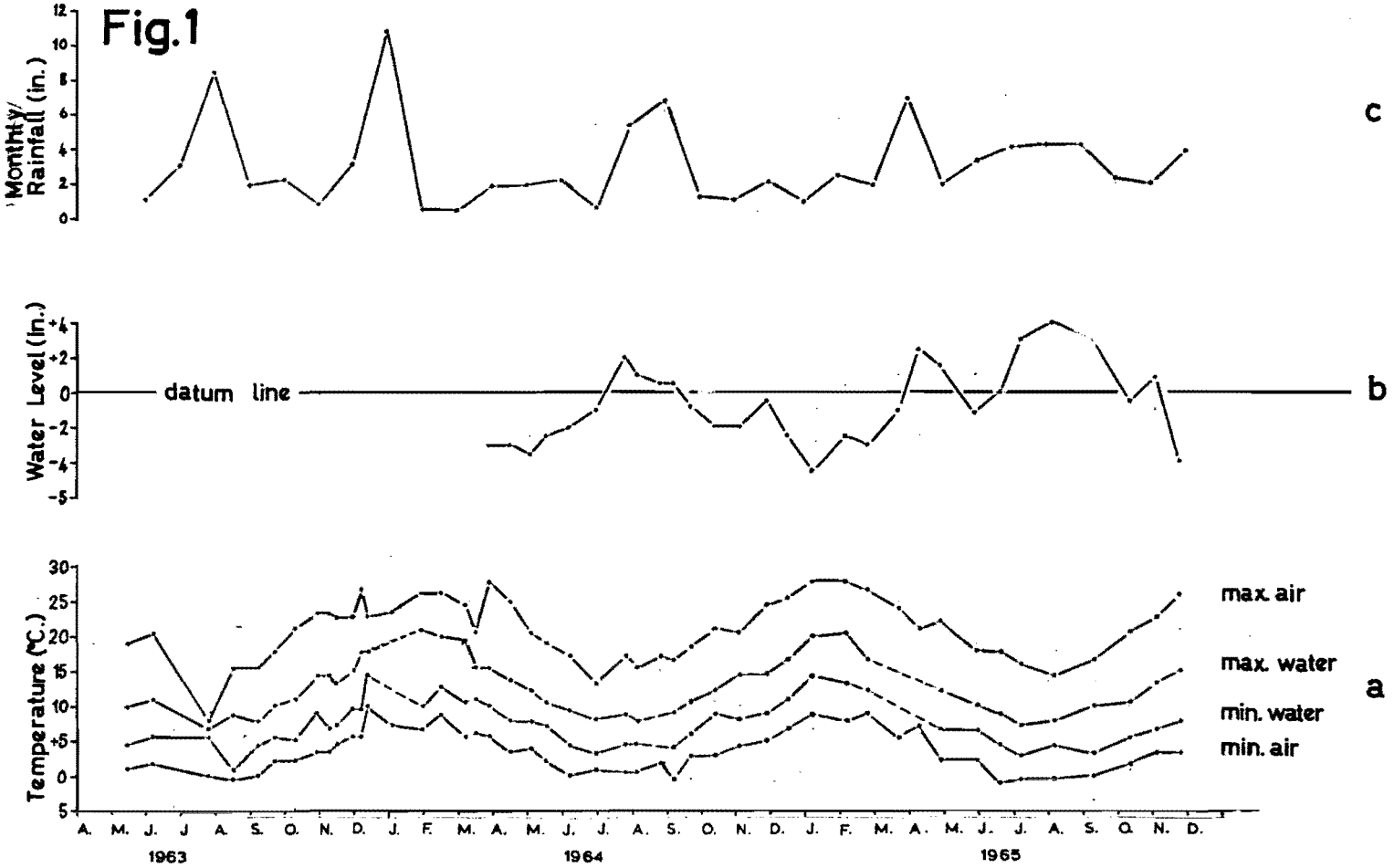
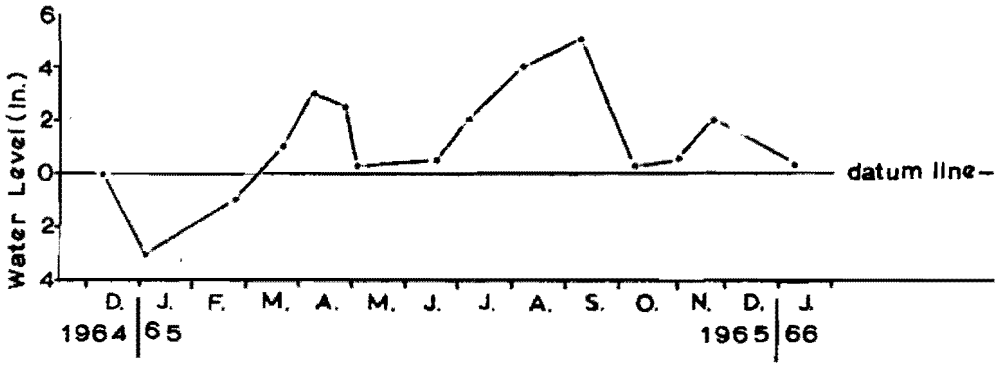

Monthly Rainfall (in.)
12
10
8
6
4
2
0
c
Water Level (in.)
+4
+2
0
-2
-4
-5
datum line
b
Temperature (°C.)
30
25
20
15
10
5
0
max. air
max. water
min. water
min. air
a
A. M. J. J A. S. O. N. D. J. F. M. A. M. J. J. A. S. O. N. D. J. F. M. A. M. J. J. A. S. O. N. D.
1963
1964
1965

Fig. 2


Monthly Rainfall (In.)
12
10
8
6
4
2
0

b


Water Level (In.)
6
4
2
0
2
4
datum line
D. J. F. M. A. M. J. J. A. S. O. N. D. J.
1964 65
1965 66

a

30-60 cm. wide and 4-10 cm. deep, at an altitude of 3000 ft. - 4500 ft. on Mount Fox (7604 ft.) ten miles north-west of Sherwood Downs, Fairlie. A series of cascades are separated by pools and swiftly flowing stretches. The stream bed is sunken 60-90 cm. below the surrounds and is overhung by tussock grasses. The rocks have heavy growths of algae and hepatics. As at Coads Creek, blepharocerid larvae are normally found only below cascades where the rocks are free of vegetation.

Discussion: The habitats of the three study areas are more typical of New Zealand blepharocerid habitats than those of the tributary to the Pu-Pu Spring River, Coads Creek and the tributary to the North Opuha River. However, all the described habitats are characterised by the following:-

1. A continuous, swift flow of clear water sufficient to keep heavy growths of algae and other plants off at least some areas of the rocks.
2. Relatively stable stream bed with embedded rocks to provide larval populations with some protection against flood scouring.
3. Rocks protruding above the water level on which adults may rest and oviposit. (The tributary to the Pu-Pu Spring River is exceptional in this case as there are no rocks protruding above the water level).

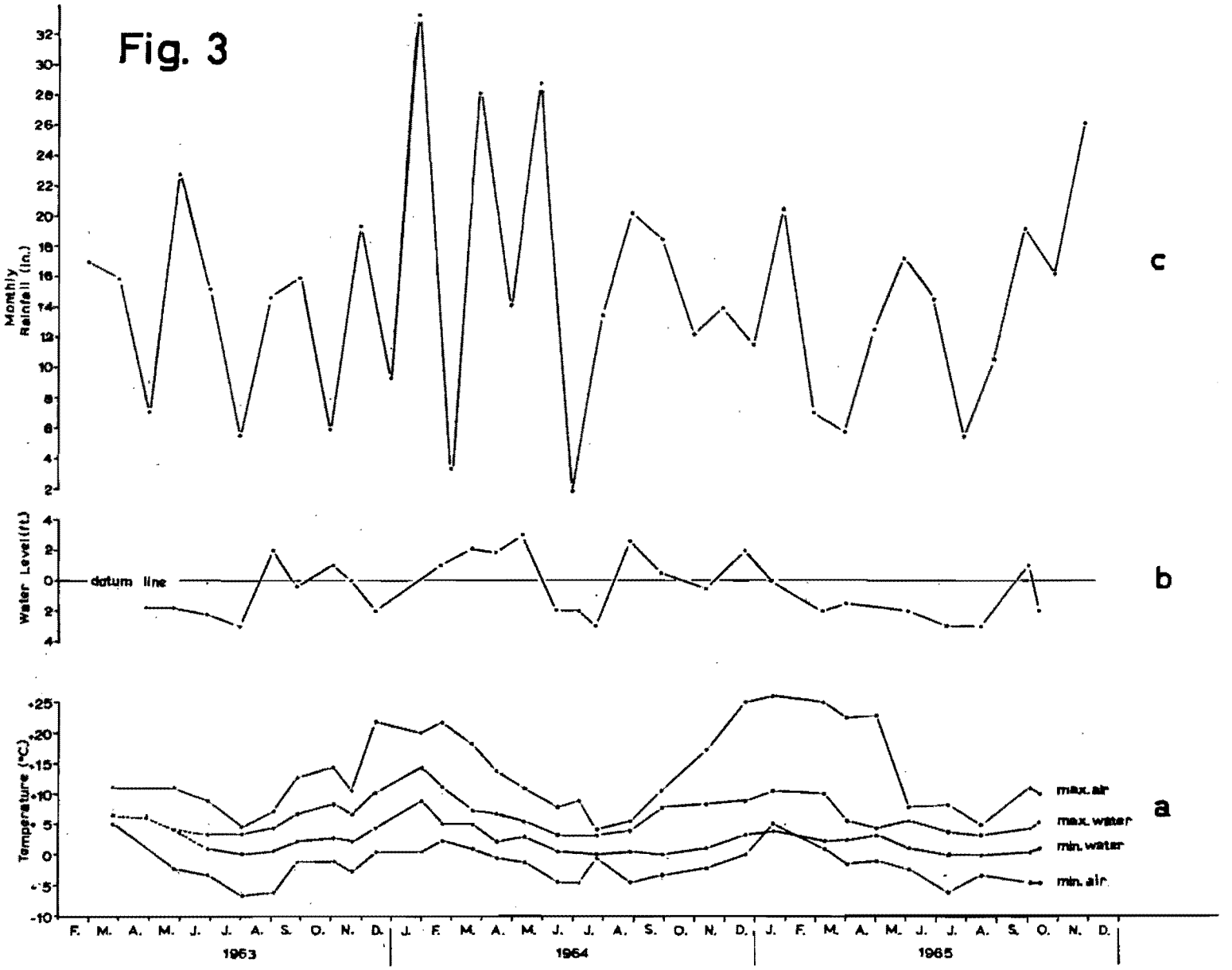
PART II. PHYSICAL FACTORS.

Temperatures.

Records of Maximum and Minimum air and water temperatures were kept at both Purau and Bealey. At Kaituna temperatures were only taken on collection days.

Purau. (Fig. 1a): Temperature records extending from April 1963 - November 1965, show that the maximum temperatures are reached between late November and early April, and the minimum

Fig. 3


Monthly Rainfall (in.)
c
Water Level (ft.)
datum line
b
Temperature (°C)
max. air
max. water
min. water
min. air
a
F. M. A. M. J. J. A. S. O. N. D. J. F. M. A. M. J. J. A. S. O. N. D. J. F. M. A. M. J. J. A. S. O. N. D.
1963
1964
1965

temperatures are reached between May and September. During this latter period, snow often lies on Herbert Peak (June-October), and has fallen as low as the study area (June 1965).

The maximum air temperature was 28°C (April 1964, January and February 1965) and the minimum air temperature -1.5°C (June 1965). The water temperatures which followed closely those of the air showed a maximum of 21.5°C (January 1964) and a minimum of 3.8°C (June-July 1965).

These records agree closely with those of Hamilton (1931) and Wisely (1962).

Kaituna: The temperatures taken during each collection indicate that the air temperatures at Kaituna and Purau are very similar. However, probably because of the greater rainfall and amount of bush cover present, the water temperature does not show as great a range as that at Purau.

Bealey Chasm (Fig. 3a): Temperatures were recorded from March 1963 - October 1965. Maximum temperatures are reached between December and February, and minimum temperatures between June and August. During the period of minimum temperatures snow commonly lies on the ground.

The maximum air temperature was 22°C (December 1963 and January 1964) and the minimum air temperature -4.5°C (June-August 1964). The water temperature which does not follow the air temperature as closely as at Purau, showed a maximum of 12°C (February 1964 and January 1965), and a minimum of just above 0°C (August 1963, June-September 1964 and June-October 1965).

The thermometer recording air temperatures was in a sheltered position (to prevent interference) and it is probable that the air temperatures quoted here do not give a true indication of the climatic extremes experienced by the study area.

Rainfall.

Private or official rain gauges were located near all the study areas so no attempt was made to compile personal rainfall records.

Purau: The average rainfall at Purau Station (Altitude 100 ft.) over the past 40 years is 31in. per annum. The monthly rainfall figures for 1963, 1964 and 1965 (kindly supplied by Mr A. Gardiner) are plotted in Figure 1c. With the exception of December 1963, the wettest period of the year is from April to September and this is also the coldest period of the year (p. 8).

Kaituna: As a considerable amount of rainfall on Banks Peninsula is from the south, the southerly facing Kaituna Valley has a higher rainfall than does the easterly facing Purau Valley. According to Wisely (1962), A.V. Barley showed that the average rainfall for Kaituna Valley at an altitude of 400 ft. was 54.5in. per annum. The monthly rainfall figures from Tophouse (altitude 750 ft.) for 1964 and 1965 (kindly supplied by Mr J.J. Murdoch) are plotted in Figure 2b.

The rainfall at Kaituna appears to be more evenly spread over the year than that at Purau.

Both A. Gardiner and J.J. Murdoch (pers. comm.) commented that 1964 was an exceptionally dry year.

Bealey: The rainfall at Arthur's Pass varies considerably from year to year. The monthly rainfall figures from Arthur's Pass Township (altitude 2420 ft.) for 1963, 1964 and 1965 (kindly supplied by the North Canterbury Catchment Board) are plotted in Figure 3c. The rainfall figures indicate that there may be a drier period during June or July and perhaps another dry period during January or February. Most of the rainfall occurs during northerly weather conditions, for of the 187 raindays during 1964, 140 were associated with northerly winds.

Water Levels.

Water levels were recorded at all three study areas. In each case the datum line was marked on an embedded rock.

Purau (Fig. 1b.): Water levels recorded from March 1964 - November 1965 show that the water levels are lower between October and January, and the higher water levels (excluding floods), occur between July and September.

Hamilton (1931) found that the lowest water levels were during March, May and June, and that the highest levels occurred during July.

During October 1951 - October 1952 Wisely (1962) showed that the lowest water levels occurred between January and April, and that the highest levels occurred during November.

These differences point to a great variation in water flow from season to season.

Kaituna.(Fig. 2a): Over the period (January - November 1965) that water levels were recorded at Kaituna River, they followed the same pattern as at Purau.

Bealey. (Fig. 3b): Water levels were recorded at Bealey Chasm from April 1963 - October 1965. Flooding in December 1963 removed the steel pipe driven into the river bed which was used as a datum line for water levels. Subsequent levels were taken from a new datum line marked on an embedded rock. The water levels recorded prior to the flood have been corrected as far as possible, to the new datum line. Records show that the lowest water levels occur during June, July and August followed immediately by a rapid rise in water level due to snow melt. For the remainder of the year water levels fluctuate but never reach the lowest levels experienced during winter.

Discussion:

Wisely (1962) showed that the water levels at Purau generally show an inverse relationship to the air and water temperatures; the water levels being lower during periods of high temperature. The water levels and temperatures from this present study show the same relationship.

However, during the present study water levels show a close direct relationship to monthly rainfall, as well as an inverse relationship to temperature, at both Purau and Kaituna (Figs. 1 and 2).

Variations in monthly rainfalls from year to year, may explain the discrepancies between the times of high and low water levels at Purau recorded during this present study and by Hamilton and Wisely. The similarities in the changes of water level of both Purau and Kaituna Streams are probably the result of the contiguous catchment areas being subjected to similar weather conditions.

Because of rapid runoff and the fewer visits, the records of water level at Bealey Chasm are more influenced by rainfall immediately preceeding the level recording than the overall monthly rainfall, and therefore do not show the expected close relationship to monthly rainfall figures (Fig. 3). Water levels at Bealey Chasm are lowest during the winter months (June, July and August) when precipitation is mainly in the form of snow which accumulates in the catchment area until the spring thaw. Temperature and water level are not so clearly related for the remainder of the year. The high water levels during August, September and October are probably due to early spring thawing, and are followed by lower water levels.

Floods.

Purau: After heavy rain the water level at Purau rarely rose more than 2 ft - 3 ft, returning to normal after 1 - 3 days. Water levels of this height only shifted the smaller stones and caused little or no damage to the aquatic life.

Wisely (1962) reported a flood, prior to 1951, of 6 ft. 7 in. above normal and V. Benzie (pers. comm.) states that a similar flood occurred during May, 1960. On 21st December, 1963 approximately 10 inches of rain fell at Purau Station. From debris left on the stream banks and in trees it was estimated that this rain had caused a flood of over 6 ft. above datum. (Plate 1b). The stream was again badly flooded during August 1964, when the water level was estimated to have risen to 5 ft. above datum line.

The effect of the flood reported by Wisely is not known, but the flood reported by Benzie, the December 1963 and the August 1964 flood badly scoured the stream bed and destroyed most aquatic life.

The December 1963 flood considerably altered the study area (Plate 1). The upper pool was filled with fine gravel and sand and shallowed to 2 - 3 in. It was also shortened. The rapids portion of the study area was lowered by 2 - 3 ft., cutting back into the downstream end of the upper pool. The overall gradient of the study area now became 5 degrees. Few of the larger embedded rocks that characterised the area earlier were unmoved.

Two weeks after the flood (4-i-64) the only blepharocerids present were small populations of larvae on the larger embedded rocks. Very little other aquatic life was found in the study area. By the 30-i-64 blepharocerid larvae were to be found in the scoured portions of the study area close to embedded rocks. Large numbers of simuliid larvae were also found in most of the suitable regions in the study area. By the 16-ii-64 eggs, larvae, pupae and adults were present in most of the suitable situations in the study area.

The August 1964 flood, though not as severe as the December 1963 flood, caused a certain amount of scouring. At the time of the flood the percentage of pupae in the pupal + larval collections was approximately 50% (Fig. 9) and had been increasing for two months previously. The flood destroyed most of these pupae, but within four months (November 1964) the percentage of pupae present had again risen to approximately 50%.

Some of the possible effects of this flood and the December 1963 flood are discussed in the section on Life Cycles (p.61).

Kaituna: No flood higher than 3 ft. above datum was recorded at Kaituna during the study period. Water levels of this height produced very little scouring.

Bealey Chasm: Flooding of the Bealey River is common and probably because of this most of the larval blepharocerid populations are found on embedded rocks. Floods of up to three feet above datum appear to have no effect on larval populations or on the river bed except to remove algal growths. Sometime during December 1963 or January 1964, a flood 10-15 ft. above datum (estimated from debris) changed the overall appearance of the river bed,although the larger embedded boulders remained stationary. Large amounts of gravel were shifted and the main channel of the river was changed from the western to the eastern side of the river bed. Many of the pupal aggregations, normal for this time of year, were scoured from the rocks by the flood. Larval and pupal populations survived only on the rocks that provided shelter from scouring.

By 22-ii-64 larvae and pupae were again to be found on most of the suitable rocks.

Kowhai River, Kaikoura: Prior to 1963, blepharocerid larvae were known to occur in the Kowhai River and in tributaries entering it at an altitude of approximately 700 ft. above sea level.

During June, 1963 a heavy flood caused scouring of the Kowhai River and tributaries. A search, on the 28-vii-63, of known blepharocerid habitats, revealed a complete lack of aquatic fauna. Conditions in the river bed at the time were extremely unfavourable, as it consisted of deep, shifting gravel.

A further search on the 19-ix-64 revealed that blepharocerid larvae were again present, at an altitude of 175 ft. in an area of river bed more stable than the rest and with a more rapid flow of water. A search of the tributaries was not possible.

Discussion.

From available evidence it appears that floods can have very marked short-term effects on the abundance and distribution of larval blepharocerids.

At Kaituna, N. chiltoni larvae are quite common on the smaller stones (less than 6 cm. in size), however, at Purau it is very rare to find larvæon stones of this size. It is suggested that this difference in larval distribution is caused by the less stable stream bed and more frequent floods at Purau; the smaller stones being more easily moved and hence denuded during a flood.

It is possible that flooding has a similar effect on the distribution of blepharocerid larvae at Bealey Chasm, for in the more swiftly flowing stretches of the river (more susceptible to scouring) the larvae are found almost solely on embedded rocks. It is only in the less swift and often shallower stretches of the river that larvae are found on smaller nonembedded stones.

Floods apart from their destructive effect on blepharocerid larval and pupal populations may be beneficial in that they remove heavy algal growths from otherwise suitable habitats.

Water Velocity.

The very swift water that blepharocerid larvae normally inhabit has been commented upon by Tillyard (1926), Imms (1925), Borror and Delong (1957), Mannheims (1935), Kitakami (1950), Dorier and Vaillent (1954) and Alexander (1963).

Measurements of water velocity at the Purau and Bealey Chasm study areas were made during the present study.

The initial measurements were with a Gurley Pigmy Current Meter (kindly lent by the North Canterbury Catchment Board). However, this type of measuring device cannot record velocities closer to the substrate than approximately 2.5 cm. therefore, later measurements were made with a Pitot Tube (calibrated at the North Canterbury Catchment Board Calibration Tank, Belfast, Christchurch. Accuracy to 2.5 cm./ sec.), which could record velocities at approximately 1 cm. above the substrate.

Measurements of velocity suggest that the lowest velocity tolerated by N. chiltoni larvae is approximately 26 cm./sec. for larvae were only found in water velocities higher than this and up to the maximum velocity recorded at Purau of 117 cm./sec. The larvae of this species occur in slower flowing water than any of the other species studied. At Bealey Chasm for example, no larvae were found in water with a velocity of less than 83 cm./sec. At Bealey Chasm the rapid stretches of the river were flowing at approximately 180 cm./sec. but at the bottom of the water fall that plunges into the Chasm proper, larvae were found in water with velocity of approximately 420 cm./sec. - the highest known water velocity yet recorded from a blepharocerid habitat.

The figures are comparable to those of Dorier and Vaillant (1954) who showed that the larvae of Cardiocrepis brevirostris could still remain attached to the substrate under experimental conditions, in a water velocity of 238 cm./sec., and to those of Feldmeth (pers. comm. 1965) who states that Blepharocera michineri larvae occur in the field in water velocities between 30-350 cm./sec.

The actual velocity experienced by blepharocerid larvae in Prandtl's layer is however, considerably less than that measured at 1 cm. above the substrate with the Pitot Tube. For in Prandlt's layer, a water layer close to the substrate, which according to Ericksen (1966) was demonstrated by Ambühl (1959) to be approximately 4 mm. thick, the velocity decreases exponentially with proximity to the substrate.

The Respiration Rates and Sucker Attachment of Larval Blepharocerids.

Respiration Rate: Because the non-movable tracheal gills and anal blood-gills are close to the substrate and hence in the lower water velocity regime of Prandtl's layer, high water velocities are probably necessary to provide sufficient ventilation of the respiratory surfaces to satisfy the high respiration rate, (B. Feldmeth pers. comm. 1965).

Ericksen (1966) while discussing benthic invertebrates and substrate-current-oxygen interrelationships states that the oxygen consumption of Blepharocera micheneri varied directly with increase of water velocity. However, B. Feldmeth (pers. comm. 1965) stated that B. micheneri showed no increase of oxygen consumption with water velocity increase, and later (pers. comm. 1966) kindly provided data which shows that, after an initial increase in oxygen consumption due to "boundary layer sweep away" of oxygen depleted water from the respiratory surfaces between 0-4 cm./sec., ~~that~~ there was no significant increase in oxygen consumption up to 30 cm./second.

Sucker Attachment: The larval sucker is an extremely efficient organ of attachment, and larvae are often damaged during efforts to dislodge them from rocks during collection. The sucker also operates when the larva is dead, a fact commented on by Tonnoir (1930). The sucker attaches to any wet surface it contacts, suggesting that its attachment is due to its shape and physical factors and does not require energy expenditure.

This conclusion fits Feldmeth's findings on the respiration rates of B. micheneri, and Feldmeth (pers. comm. 1966) believes that the sucker attachment mechanism suggested above may partially explain the constant respiration rate despite increasing current. This may also explain why blepharocerid larvae can remain attached indefinitely to rocks in water velocities of up to 450 cm./sec.; conditions which few other insects with different methods of attachment can withstand.

Oxygen Saturation of Water. (Table 1).

Mannheims (1935) believed that blepharocerid larvae in choosing rapidly flowing water were in fact selecting sufficiently oxygenated water for their respiratory requirement. However, Kendeigh (1961) and Reid (1961) have pointed out that the oxygen supply in most streams is usually ample for insect life and that the oxygen concentration in rapids is not very different from that in smoother flowing stretches of water.

Table 1.

Oxygen Saturation of Water.

Date	O_2 in parts per million.	% Saturation.
Bealey Chasm.. 2600 ft.		
14-xii-63	11 at 7.8°C.	100
1-ii-64	6.6 at 8.5°C.	100
22-iii-64	11 at 5.8°C.	95
12-v-64	10 at 5.6°C.	86
16-vi-64	13 at 3°C	106
17-vii-64	11 at 3°C.	91
Temple Basin.		
15-xii-63 5130 ft.	11 at 3.5°C.	100
22-iii-64 4500 ft.	7.5 at 6°C.	72
Mingha River. 2750 ft.		
16-xii-63	11 at 10°C.	110
Purau. 10 ft. (Wisely 1962).		
1-x-52	11.6 at 17°C.	120
Purau. 250 ft.		
7-ix-63	9 at 15.6°C.	85
16-ii-64	7 at 17.2°C.	73
28-ii-64	9 at 12.2°C.	83
14-iv-64	10 at 12.2°C.	85
3-v-64	12.5 at 10°C.	110
16-v-64	11 at 6.7°C.	84

Dissolved oxygen concentrations were measured at various times with a B.D.H. Lovibond Nessleriser and Comparator (accuracy approximately 1 p.p.m.) at Purau Stream, Bealey Chasm and other localities. The % oxygen saturation was calculated from Rawson's Nomograph taken from Reid (1961).

Sufficient measurements were made to establish the generally high oxygen saturation of the three study areas, and therefore it was thought unnecessary to examine either the diurnal or seasonal variation in oxygen saturation. Water at high altitude and low temperature is often supersaturated with oxygen (Mani 1962), and this characteristic of alpine waters combined with the torrential nature of the river at Bealey Chasm probably keeps the % saturation of oxygen generally high. Temple Basin and Mingha River, both in the Arthur's Pass region, also show high % saturation levels of oxygen.

Purau generally shows lower levels of oxygen saturation than the Bealey River. This would be expected from the general nature of the stream bed (i.e. less torrential than the Bealey River) and the larger amounts of fauna present. However, Wisely (1962) recorded from Purau a saturation of 120%, and during the course of this study a saturation of 110% was recorded (3-v-64). Records show that the day was fine, warm and that the stream had heavy growth of algae, so that it is likely, as Reid (1961) has shown, that the oxygen supersaturation was caused by algal photosynthesis.

Dissolved Solids and pH (Table 2).

Dissolved Solids: In an attempt to correlate the occurrence of algal growths at Bealey Chasm to other factors besides water level and temperature (p.21), samples of water were taken and analysed by the Government Analyst, Chemistry Division, Department of Scientific and Industrial Research, Christchurch.

The analyses show that Bealey Chasm water is low in dissolved solids. A similar result to that obtained by Rowley-Smith (1961) for a sample of water from Sudden Valley, Hawdon River, Arthur's Pass region.

Table 2.

	Bealey Chasm.								Sudden Valley*	Purau **
	28-ix-63	21-xi-63	1-ii-64	22-iii-64	12-v-64	16-vi-64	1-x-64	20-i-65	7-xi-61	1-x-52
pH. Spot.	6.9		6.4	6.6	6.2	6.6	6.4	6.8		
Analyst.	7.1	7.0	7.1	7.2	6.5	7.1	6.9	8.1	7.3	7.3
Parts per million.										
Chlorine in chlorides.	2	2	-	1	T	-	2	-	2	19.0
Nitrate Nitrogen.	-	-	-	-	-	-	-	-	-	0.4
Nitrite. Nitrogen.	-	-	-	-	-	-	-	-	-	-
Ammoniacal Nitrogen.	.054	.038	.005	.003	-	-	-	-	-	-
Albuminoid Nitrogen.	-	.006	-	-	.01	-	-	-	-	T
Total Iron.	-	-	.16	.16	.2	.08	-	.24		0.15
Total Hardness.	23	16	18	17	7	17	13	27		34
Methyl Orange Alkalinity.	20	20	15	14	6	13	8	18		
Calcium.							10	27		15
Magnesium.								-		19
Phosphate.	T	T	-	-	T	-	-			
Silica.	-	-	-	4	-	-	2	-		
Sulphate.					2					

* Rowley-Smith (1962) ** Wisely (1962)

According to C.J. Burrows (Botany Department, University of Canterbury, pers. comm.) the low content of dissolved solids in the water is not surprising in view of the high rainfall and rapid runoff in the Arthur's Pass region.

There are no obvious trends in concentration of any of the dissolved solids examined that might account for the variation in the algal growths. The sudden decrease of Total Hardness and Methyl Orange Alkalinity on 12-v-64 may be due to the flood conditions when the sample was taken.

It was not possible during the course of this study to have analyses made on the water from either the Purau or Kaituna study areas. However, Purau Stream was examined by Wisely (1962) and his data show the water to be generally similar to that at Bealey Chasm except for the high chloride content due to sea spray deposition.

pH: At both Purau and Bealey Chasm, pH values were determined regularly using a Lovibond pH Comparator. (This method of determining pH is highly recommended for field use because of the robust nature of the apparatus). The average pH value at Purau was 7.0, ranging from 6.7 (23-vii-64) to 7.3 (6-i-65).

The average pH value at Bealey Chasm was 6.6, ranging from 6.2 (12-v-64) to 6.9 (9-iii-65). The "spot" pH values taken at the same time as the water samples for analysis, are lower than those determined by the Government Analyst, in one case the difference is startling, 6.8 versus 8.1 on 20-i-65. These differences may be due to different methods of pH determination, but seem more likely to be due to changes within the sample before analysis was carried out.

Records of pH values from other blepharocerid localities in the South Island, show that the majority of streams and rivers have a pH of 6.8, with the remainder ranging from pH 6.1 - 6.3. The Cleddau River, Milford Sound, a blepharocerid locality, sampled on the 19-i-66 during heavy rain, showed a pH of 5.2.

Both Carpenter (1928),and Macan and Worthington (1951) point out that tolerance to pH depends on many other factors, and Macan and Worthington state that pH only gives a very rough indication of conditions present and that its importance is not so great as was formerly thought.

It is unlikely therefore that pH has any great effect on the distribution and biology of New Zealand blepharocerids.

PART III. BIOTIC ASSOCIATES.

Floral associates.

Purau and Kaituna: Hepatics and mosses are abundant in the study area at Kaituna, but were not present at Purau probably because of the more frequent floods. However, at Purau and to a lesser extent Kaituna heavy growths of algae occurred during the summer months (December-February). This was particularly noticeable after the December, 1963 flood at Purau. A sample of the algal growth taken from the rocks at Purau on the 30-i-64 contained the following algae (identified by Dr E.A. Flint, Botany Department, University of Canterbury). Symbols used to indicate abundance are:- V.R. = very rare; R. = rare; R.C. = rare to common; C. = common; V.C. = very common; A. = abundant.

Navicula spp (A), Nitzschia sp. (V.C.), Gomphonema spp (C), Cymbella sp. (R.C.), Melosira sp. (R.C.), Cocconeis sp. (R.), Oscillatoria sp. (R.), Synedra sp. (R.), ?Ankistrodesmus sp. (V.R.).

According to Wisely (1962) Stauroneis phoenicentron and Amphora ovalis are also present at Purau.

During the winter months the higher waterlevels at Purau keep the stream bed free from noticeable algal growth.

Bealey Chasm: During the summer months (January and February) long "streamers" of filamentous green algae containing Ulothrix sp. and Spirogyra sp. grow in the slower flowing stretches of the study area. This growth is removed if flood levels rise more than 3 ft. above datum.

During the winter months and particularly when the water level is low and relatively constant (June and July) (Fig. 3b), the reddish-brown coloured Entophysalis nivularis nivularis (=Chamaesiphon) covers most submerged rocks. This growth is mainly removed by spring floods in August and September. According to Dr E.A. Flint (pers. comm.) and Whitford and Schumacher (1963) the Entophysalis spp are typical of swiftly flowing water. Other algae collected from Bealey Chasm are Diatoma hiemale and Synedra sp.

Epizooic Algae: It is well known that the dorsal surface of blepharocerid larva is often covered with epizooic algae (Gomphonema and Nitzchia on Blepharocera capitata, Kellogg 1902; Ceratoneis arcus on Liponeura cinerascens and Hapalothrix lugubris, Mannheims 1953; and epizooic algae on New Zealand blepharocerid larvae, Dumbleton 1963a).

Collections from Purau, Kaituna and Bealey indicate that epizooic algae are the same species as those covering the rocks on which the blepharocerid larvae live. Thus Melosira and Gomphonema are the most common epizooic algae on larvae from Purau, while Entophysalis and Diatoma are the most common algae on those from Bealey Chasm.

These growths, particularly of Gomphonema and Entophysalis, often become extremely luxurious and completely cover any features on the dorsal surface of the larva. The most extensive growth was that of Gomphonema on N. hudsoni larvae taken from Ryton Stream, Lake Coleridge on 10-ii-63.

Faunal Associates.

Only fauna found in the same habitats as the larvae, pupae and adults, from the three study areas is considered, even though distinct faunas do occur, with blepharocerid larvae and pupae elsewhere particularly in the smaller streams, at high altitude.

For the following identifications I am indebted to:-
Mr P.M. Johns - Tipulidae
Zoology Department, University of Canterbury.

Mr A.G. McFarlane - Rhyacophilidae
Canterbury Museum.

Mr J.G. Penniket - Ephemeroptera
Canterbury Museum. Plecoptera

Associates of Larvae and Pupae.

Purau: The turbellarian Dugesia montana and the gastropods Potamopyrgus corolla and P. antipodium, though occurring in the study area, were rarely found on the same stones as N. chiltoni larvae and pupae. The most common larval and pupal associates were ephemeropteran nymphs:- Deleatidium spp. including D. myzobranchia, Zephlebia (Z.) vesicolor, Coloburiscus humeralis and Nesameletus ornatus. Only one nymph of the carnivorous plecopteran Stenoperla prasina was found, though the nymphs of Austroperla cyrene, Aucklandobius triavacuata (=Nesoperla), Zealandoperla decorata and Zealandoperla sp., were relatively common. Occasionally the voracious larvae of the neuropteran Archichauliodes diversus were collected near the banks of the study area. The trichopteran larvae Helicopsyche sp., Hydopschye sp. and Olinga feredayi were often very common on the under surface of the rocks. The carnivorous rhyacophilid larvae Costachorema psaroptera, Hydrobiosis parumbripennis and

Psilochorema sp. were less common.

The simuliid larvae Austrosimulium tillyardi occurred in very large numbers on the upper surface of the stones, during the spring and early summer (September, October and November).

During November 1963 and 1965 small, unidentified, red larval mites were found in depressions on rough textured rocks, with the earlier instars of N. chiltoni. This appears to be the first record of such a mite from Purau Stream.

A more complete list of aquatic fauna occurring in Purau Stream is given by Wisely (1962).

Kaituna: The aquatic fauna in the Kaituna River study area was very similar to that in the Purau study area. However, there were fewer Austrosimulium tillyardi larvae and the small aquatic mite was never discovered.

Bealey: Compared with Purau and Kaituna, the fauna that occurs on the rocks with blepharocerid larvae and pupae at Bealey Chasm is impoverished both in species composition and number. The ephemeropteran nymphs Deleatidium (Deleatidium) sp., D.(undescribed subgenus) sp. and Nesameletus ornatus, as well as the plecopteran nymphs Zelandobius sp. and Aucklandobius sp. are the most common faunal associates. The trichopteran larvae Costachorema psaroptera, C. brachyptera and the simuliid larva Austrosimulium sp. (sp. 1 of ungulatum group. Dumbleton 1963b) occur only rarely.

The commensal chironomid Dactylocladius commensalis is discussed later (p.25).

Associates of Adults.

The following adult insects were collected from places frequented by blepharocerid adults.

Purau and Kaituna: From October to January, at both Purau and Kaituna, tipulids were found in large numbers resting or flying with N. chiltoni adults. Both Gnophomyia sp. and Dicranomyia fasciatia were found at Purau but only the latter at Kaituna.

The ephemeropteran adults Deleatidium myzobranchia and Deleatidium sp. as well as the plecopteran adults Zealandoperla confusus and Zealandoperla sp. are also common during the summer months.

During January the empids Trichopezia sp., Ceratomerus prodigiosus, some other unidentified empid species, the mycetophylid Allodia sp. and unidentified chironomid adults are common.

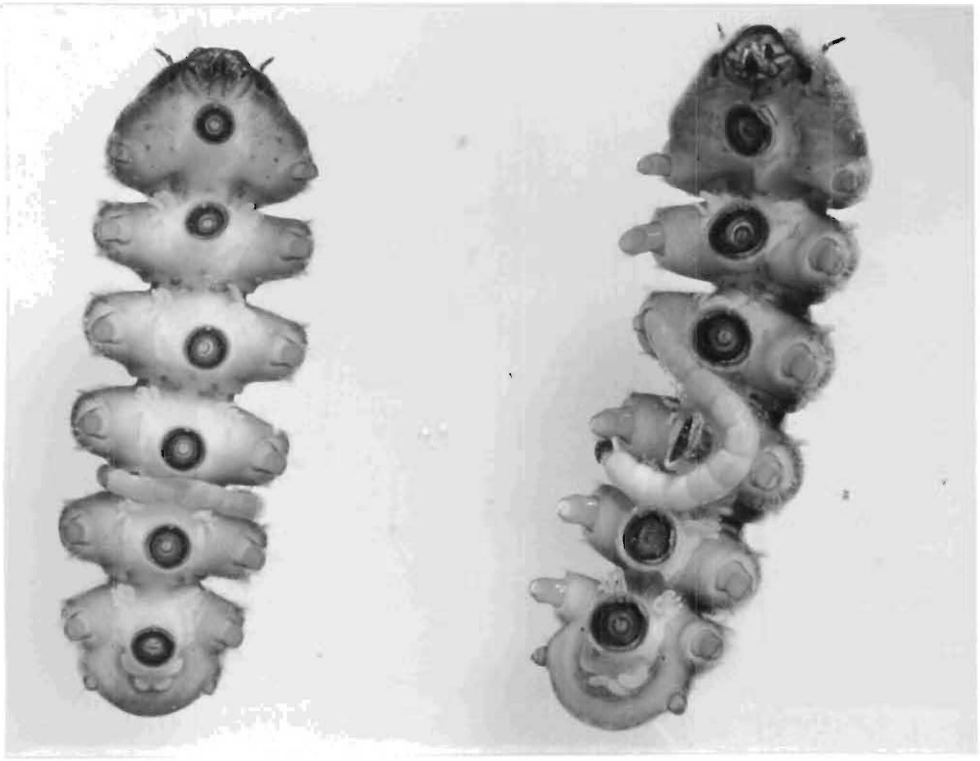
Bealey: No tipulid adults were collected with blepharocerid adults at Bealey Chasm though they occurred in great profusion in the vegetation along the banks of the study area.

The following ephemeropteran adults were common from November to January:- Deleatidium (D.) autumnali. Deleatidium (D.) myzobranchia, Deleatidium (D.) sp., Nesameletus ornatus, Nesameletus sp., and Oniscigaster distans. During December and January the plecopteran adults Spaniocerca sp. and Zealandoperla sp. as well as the empids Trichopeza longipennae and Trichopeza sp. were common. Trichopeza adults resemble closely the blepharocerid adults at Bealey Chasm both in flight pattern and in general morphology. It is suggested here that mimicry may be involved. Hora (1930) has commented that the empid Clinocera is very similar to and occurs with some Indian blepharocerid adults. The bibionid Philia sp. (=Diphorus) was collected

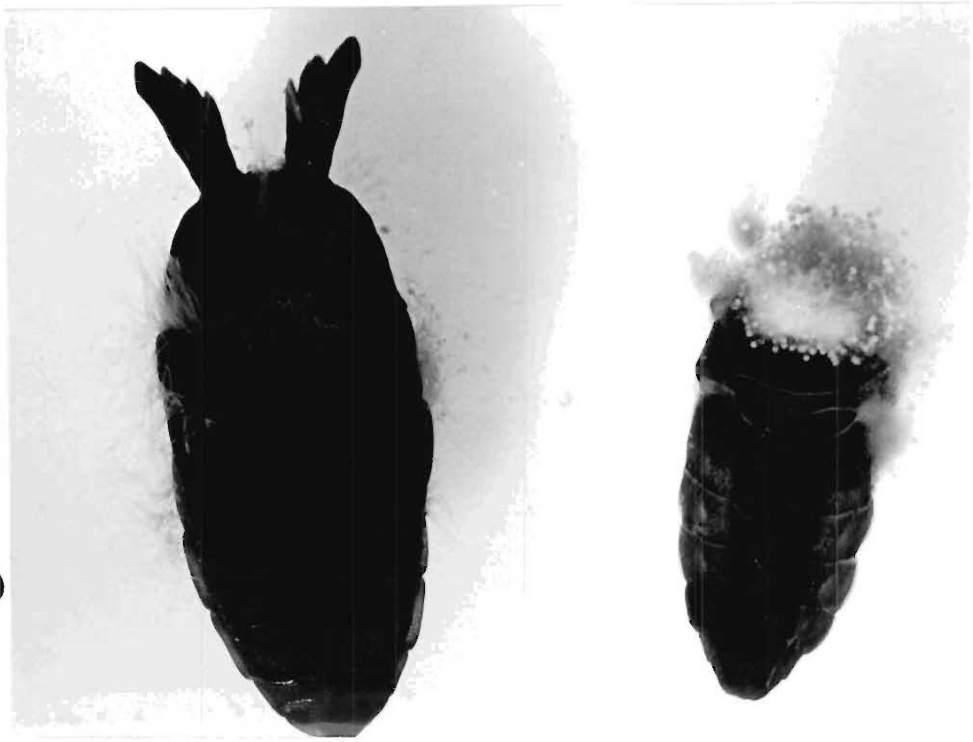
PLATE 4.

(a) Larvae of *Dactylocladius commensalis* on larvae of *N. campbelli* (left) and *N. hudsoni* (right).

(b) Pupae infected with *Saprolegnia* sp. (left) and *Aquamortierella elegans* (right).



a



b

during November. Occasionally during the summer months the adults of the commensal Dactylocladius commensalis were collected.

Commensals.

The close association between the larvae of N. hudsoni and the larvae of the chironomid Dactylocladius commensalis was first described by Tonnoir (1923). Both Tonnoir and Dumbleton (1963a) believed the association to be specific to N. hudsoni, but later collections during the course of this study show that the association is mainly within the hudsoni-complex but that the chironomid does occasionally occur with N. campbelli (Chpt. I).

No D. commensalis larvae have been found on first instar blepharocerid larvae, in any species, and the association appears to begin with the second instar.

The chironomid larva is normally curled around one of the suckers or body divisions of the blepharocerid larva, or intertwined between two or three suckers (Plate 4a). Usually one chironomid larva, but more rarely two, occur on a blepharocerid larva. The occurrence of three larvae on the same blepharocerid is very unusual, as also pointed out by Tonnoir (1923).

The chironomid larva secretes a gelatinous sheath which adheres to the blepharocerid larva and eventually is used to attach the chironomid pupa in the same position.

Tonnoir (1923) and Dumbleton (1963a) have pointed out that the life-cycle of D. commensalis must be so organised as to allow the larva to pupate and the adult emerge before the blepharocerid pupates.

Attempts were made to follow the frequency of occurrence of D. commensalis larvae on the blepharocerid larvae at Bealey Chasm. However, collections soon showed that D. commensalis is only a facultative commensal and occurs on the rocks as well as on the ventral surface of blepharocerid larvae. The chironomid larvae are also more resistant to killing fluids than are

blepharocerid larvae and tend to leave the gelatinous sheath and the blepharocerid larva completely before death. The presence of the transparent gelatinous sheath is very difficult to ascertain and it was virtually impossible to determine the exact number of commensal chironomid larvae in a sample.

However, samples fixed with Carnoy's Fluid which kills both larvae more rapidly than the normally used arthropod fixative, indicate that the frequency of occurrence could be as high as 37% (30-ix-64), but generally throughout the year was approximately 10%.

Parasites.

Fungi: Dead blepharocerid pupae at Purau and Bealey, normally become infected with the Phycomycete Saprolegnia sp. This saprophytic fungus appears to enter the dead pupa by way of the spiracle at base of the pupal horns and ramifies the body with hyphae. The mycelium bursts through the intersegmental membranes, especially along the dehiscence line on the prothorax. The gemmae are characteristically borne on the hyphae protruding from these splits (Plate 4b).

At Bealey Chasm the pupal aggregations are,in addition, often infected with another Phycomycete that appears to be a facultative parasite. This fungus appears initially to infect dead pupae but then spreads to adjacent healthy pupae. The mode of entry into the pupa and the bursting open of the pupal case is similar to that of Saprolegnia.

The sporangiophores and sporangia of this parasitic fungus are very similar to those of Rhizopus (bread mould), (Plate 4b), but the spore shape is distinct and Professor R. Emerson (Botany Department, University of Berkeley, California, pers. comm. 5-v-64) stated that the fungus represents a new genus of Mucorales. Subsequent attempts by Emerson to isolate and culture the fungus were unsuccessful.

However, the fungus will be described by R.W. Embree (Botany Department, Brown University, Rhode Island) in collaboration with H. Indoh as Aquamortierella elegans gen. et sp. nov. The following description will be published in the American Journal of Botany, early 1967, and was very kindly provided by R.W. Embree:- Aquamortierella elegans gen. et sp. nov.

Hyphae much branched, 1.5-6.5 μ dia, numerous vesicles present, vesicles up to 30 μ dia. Sporangiophores arising from substrate mycelium, single or clustered, simple, erect, non-septate, 340-930 (Av. 560) μ long, obclavate, tapering from 28-65 (av. 45) μ basal dia. to 21-46 (av. 36) μ apical dia. Apophysis conspicuous to absent, 36-70 (av. 56) μ dia. Sporangia solitary, spherical, 63-158 (av. 100) μ dia. Columella inconspicuous to absent, up to 17 μ high. Spores reniform to sinuate-allantoid, 13-23 (av. 18) μ long, 4-8 (av. 5.8) μ dia, apically appendiculate. Spore appendages simple, vermiform, 20-35 μ long, 1.5 μ dia. at tip. Sexual spores unknown. Habitat: fresh water; on Neocurupira pupae, New Zealand; hemp seeds, Japan.

According to Embree (pers. comm. 23-v-66), H. Indoh has collected A. elegans from hemp seeds in Japan.

Table 3. Abundance of Fungal Parasites at Bealey Chasm.

Date.	Aquamortierella	Saprolegnia	Number of Pupae.
15-xii-62	-	6.0%	50
24-iii-63	2.0%	6.0%	50
28-iv-63	-	18.5%	195
16-vi-64	2.3%	46.0%	43
9-iii-65	11.2%	8.9%	89

Saprolegnia is the most abundant fungus on the pupal aggregates at Bealey Chasm.

The greatest abundance of Aquamortierella and Saprolegnia occurs during low water periods (Fig. 3b), and may indicate that many pupae are killed or weakened by exposure to the air, for Madelin (1966) states that normally harmless and saprophytic fungi can become parasitic on stressed or injured insects.

Nematodes: Craig (1963, see App.I) reported on the occurrence and effect on the host of the nematode Agamomermis sp. in the pupae and adults of Neocurupira campbelli and Peritheates turrifer. Since then Agamomermis has been found in the adults of Neocurupira hudsoni and N. tonnoiri. Further examination of parasitised N. campbelli adults has shown that the nematodes cause castration, for parasitised males exhibit the female antennal segment number (Chpt. I) and females fail to develop eggs. In brachypterous N. campbelli females, the nematode usually occupies the thoracic space normally filled with wing muscles.

Determination of the % occurrence of nematodes in pupae, by dissection, showed at Bealey Chasm a range of infection of Agamomermis from 0-12%.

The other stages in the life cycle of Agamomermis are not known.

Acarina: Mites are known to occur on the adults of many insects in New Zealand but there appears to have been little published concerning this relationship. In one of the few papers Burrows (1961) records mites on Diptera, Lepidoptera and on Cicadas (Homoptera) in the Arthur's Pass region from altitudes of 4000 ft. to 6000 ft.

Red parasitic mites have been taken from the adults of Deleatidium myzobranchia, Trichopeza longipennae, Neocurupira campbelli and N. hudsoni at the Bealey Chasm study area. The mites on the empid T. longipennae and on the blepharocerid adults were identified by Dr V.M. Stout (Zoology Department, University of Canterbury) as Hydryphantes sp. The mites appear to bury their mouth parts in the host producing a very strong attachment. They may attach to any part of the body of the host but they are more commonly found on the articular membranes of the thorax than elsewhere on the body. Usually there are 2-3 mites on each adult host insect but one N. campbelli male was parasitised by 21 mites, and showed no apparent effects from this heavy infestation.

The life cycle of Hydryphantes sp. at Bealey Chasm is unknown.

Red mites (possibly Hydryphantes) have been observed on the rocks near to pupal aggregations and near to resting blepharocerid adults. It is probable that infestion occurs under such conditions.

Predators.

Predators of Larval blepharocerids: Reported predators of blepharocerid larvae include Rhyacophilidae larvae, fish and birds (Mannheims 1935, Wesenberg-Lund 1943 and Alexander 1963).

The only known predators of New Zealand blepharocerid larvae are nymphs of the plecopteran Stenoperla prasina, the larvae of Archichauliodes diversus (Neuroptera) and Rhyacophilidae larvae.

The larvae of S. prasina and A. diversus are only rarely found with blepharocerid larvae and therefore are probably not important predators. Gut analyses of the few Archichauliodes larvae collected suggests Ephemeroptera nymphs are taken in the same

Table 4.

Gut contents of Predators.

Date.	No. specimens examined.	Ephemer-optera	Chiron-omidae.	Simul-iidae.	Blephar-oceridae.	Others.
Archichauliodes.						
December 1962- November- 1965.	5	++	-	-	++	-
Rhyacophilidae.						
9-xii-62	2	+	-	-	-	+
3-i-64	3	+	-	+	-	+
3-ii-63	4	+++	-	+	++	-
8-iii-64	2	+	-	+	-	-
15-iii-64	1	-	+	+	-	-
3-v-64	5	++	+	++	++	-
17-v-64	1	+	-	-	-	-
3-xi-64	1	-	+	-	-	-
9-xii-64	2	+	+	+	-	-
14-xii-64	1	-	-	+	-	-
6-i-65	4	++	-	++++	+	-
8-v-65	1	-	-	-	+	-
10-v-65	1	+	-	-	+	-
24-xi-65	2	+	-	-	+	+
Totals	30	14	4	12	8	3

* Indicates presence in gut.

proportion as blepharocerid larvae (Table 4).

The rhyacophilid larvae Costachorema psaroptera, Hydrobiosis parumbripennis and Psilochorema sp. were commonly collected with blepharocerid larvae at both the Purau and Kaituna study areas. Rhyacophilidae were uncommon at the Bealey Chasm study area and only a single C. psaroptera larva was collected there.

The rhyacophilid larvae move over the rocks and while remaining attached with the pygopods make rapid lunges at blepharocerid and other insect larvae. Smaller blepharocerid larvae when caught are lifted off the substrate and eaten whole, while larger larvae are held against (or cannot be pulled free from) the substrate and are torn into chunks by the powerful chelate forelimbs.

Gut analyses of rhyacophilid larvae from the Purau and Kaituna study areas show that although blepharocerid larvae appear to be one of the principle constituents of the rhyacophilid diet, Ephemeroptera nymphs and Simuliidae larvae are present more frequently (Table 4).

The fish Galaxias maculatus, Galaxias fasciatus and Gobiomorphus gobioides are known to occur in Purau Stream (Wisely 1962 and Benzie 1961), but none were taken during this study in general collecting. As far as is known (M.C. Burnett, Fisheries Research Laboratory, Christchurch. pers. comm.) blepharocerid larvae have never been recovered from gut contents of fresh water fish in New Zealand.

Predators of pupal blepharocerids: The fully hardened pupal case of blepharocerids can withstand the attacks of rhyacophilids, though the pupal horns are often damaged. The newly formed pupa with its soft cuticle is not so protected and this stage is subjected to predation by rhyacophilid larvae. Costachorema psaroptera have been observed attacking newly formed N. chiltoni pupae in the laboratory. After a hole had been torn in the pupal case the head was inserted and the soft internal material eaten.

Empty pupal cases with jagged holes torn in the dorsal surface were collected from all study areas, and this damage is probably caused by rhyacophilid larvae. Tonnoir (1924) reported that many pupae of the Tasmanian blepharocerid Edwardsia ferrunginea had been attacked by predators, for they showed jagged holes on the dorsal surface.

Predators of blepharocerid adults: Spiders are the only known predators of adult blepharocerids in New Zealand.

At Purau, Kaituna and Bealey Chasm, blepharocerid adults are often found caught in spider-webs close to the water edge.

Lycosid spiders are numerous at Purau during the mid-summer months. Although these spiders have been observed snatching N. chiltoni adults as they flew past rocks to the water edge, they were not normally found near to positions frequented by N. chiltoni adults.

Empid adults are often collected flying with blepharocerid adults, particularly at Bealey Chasm. It is possible that these flies, known to be predaceous on dipterous adults (Imms 1957), attack the adult blepharocerids, but this has never been observed.

Discussion.

An examination of associates of blepharocerid larvae at Purau and Bealey Chasm shows that only the alga Synedra and the insects Nesameletus ornatus and Costachorema psaroptera are common to both study areas.

Compared with Purau the associated flora and fauna at Bealey Chasm are impoverished.

This is probably a direct result of the lack of sheltered situations for associates and of the high water velocity in this alpine habitat at Bealey Chasm.

At Purau the lower water velocities allow heavy growths of algae, particularly during summer, on otherwise suitable blepharocerid habitats. This may possibly be one of the main factors producing the relatively low larval density at Purau compared with that at Bealey Chasm where continual high water velocity and flood scouring keeps larval habitats free from heavy algal growths. Scouring during floods probably plays an important part in the maintenance of larval habitats.

Because of the density of larval associates at Purau, blepharocerid larvae may possibly have to compete with, other herbivores such as Ephemeroptera larvae for food, and with Simuliidae larvae for space.

Predators on larval blepharocerid, in particular Rhyacophilidae larvae, are more numerous at Purau than at Bealey Chasm, but their effects on the larval populations are unknown.

The most commonly found blepharocerid parasites, particularly at Bealey Chasm, are fungi and nematodes; the former causing mortality of pupae at times, the latter causing parasitic castration and loss of reproductive potential.

In general the density of blepharocerid larval populations is lower in habitats where the density and diversity of the associates is high, such as at Purau, and higher in the more rigorous conditions such as at Bealey Chasm.

In summary it appears that the larval populations may possibly be limited by the following:- heavy algal growths in areas of slowly flowing water, competition for food and space, and the effects of predators and parasites.

PART IV. BEHAVIOUR.

Larval Distribution.

Both the bed morphology and the larval distribution differs between the Purau and Bealey Chasm study areas. It is not clear whether the difference in distribution is due to the bed morphology or to a species difference in larval behaviour.

Overall larval distribution in both study areas appears to be limited by water velocity; larvae at Purau are found in water where the velocity is above 26 cm./sec. but at Bealey Chasm they only occur in areas where it is above 83 cm./sec.

Other factors considered, as well as water velocity, that may affect larval distribution are rock size, rock texture and adult behaviour.

Purau and Kaituna:

The pupal and larval distributions of N. chiltoni are considered together in this section as the pupae of this species do not form pupal aggregations as do those at Bealey Chasm. Larvae occur on relatively smaller stones at Kaituna than at Purau, but in general the distribution of larvae and pupae in these two study areas is similar.

The distribution of the various instars was examined quantitatively by counting all the larvae and pupae per stone in a quadrat of 3 sq. m. in the rapid portion of Purau study area (Plate 1a).

Table 5.

Distribution of larval and pupal instars at Purau.

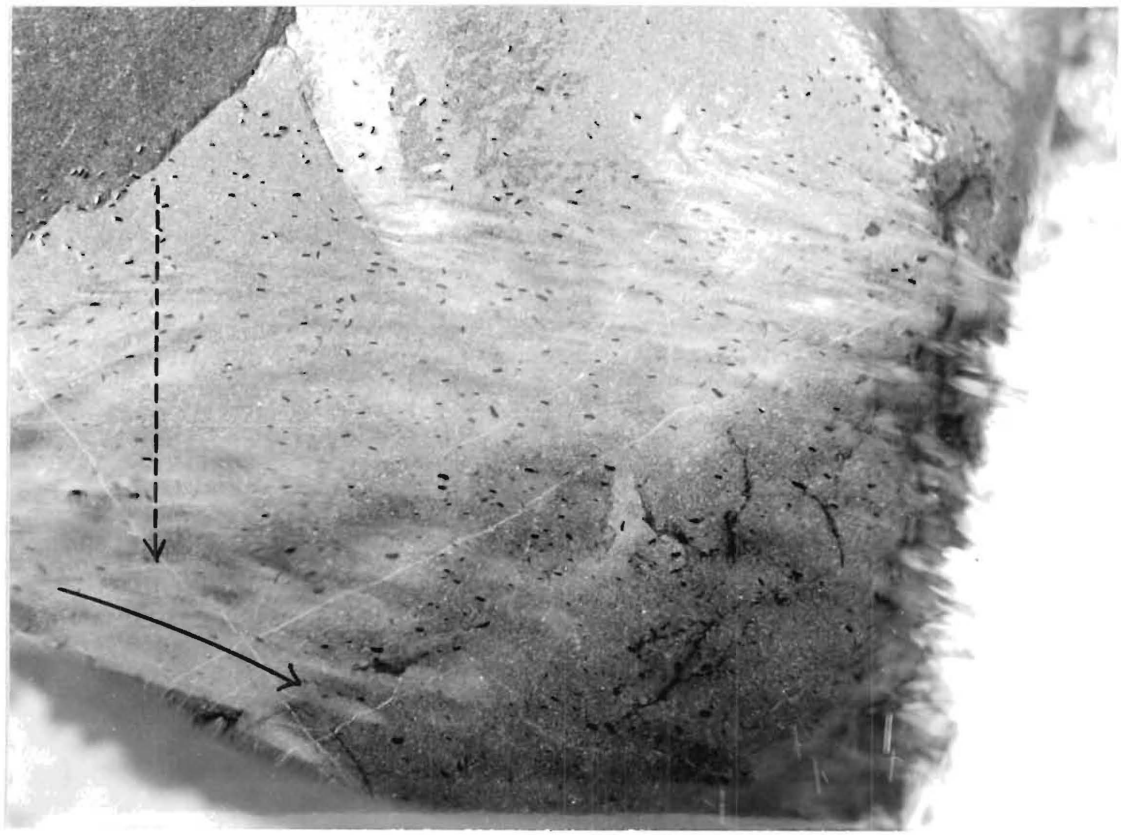
Instar.	No. of rocks bearing instar.	Total no. of each instar.	Highest % of total on one rock.
First.	8	98	81.0
Second.	8	35	39.9
Third.	20	71	16.6
Fourth.	35	106	7.5
Pupal.	25	151	14.6

Total number of rocks sampled = 44.

The results (Table 5) show that the first instar larvae occur on only a few rocks and that the number per rock is extremely variable. This agrees with observations that the majority of first instar larvae remain close to the empty egg cases and that females oviposit only on particular rocks. Second instar larvae generally occur on the same rocks as the first instar larvae, but are more evenly distributed. This indicates a limited dispersal from hatching sites. Although third and pupal instars are more evenly distributed and occur on a larger number of rocks, aggregation is still common. Only the fourth instar larvae appear to be evenly distributed.

Larvae at Purau were absent from rocks smaller than approximately 15 cm. in size. This may well be due to the movement of smaller rocks during the frequent flooding, for a careful analysis showed no relationship between the number of larvae and pupae and rock size for rocks larger than 15 cm.

a



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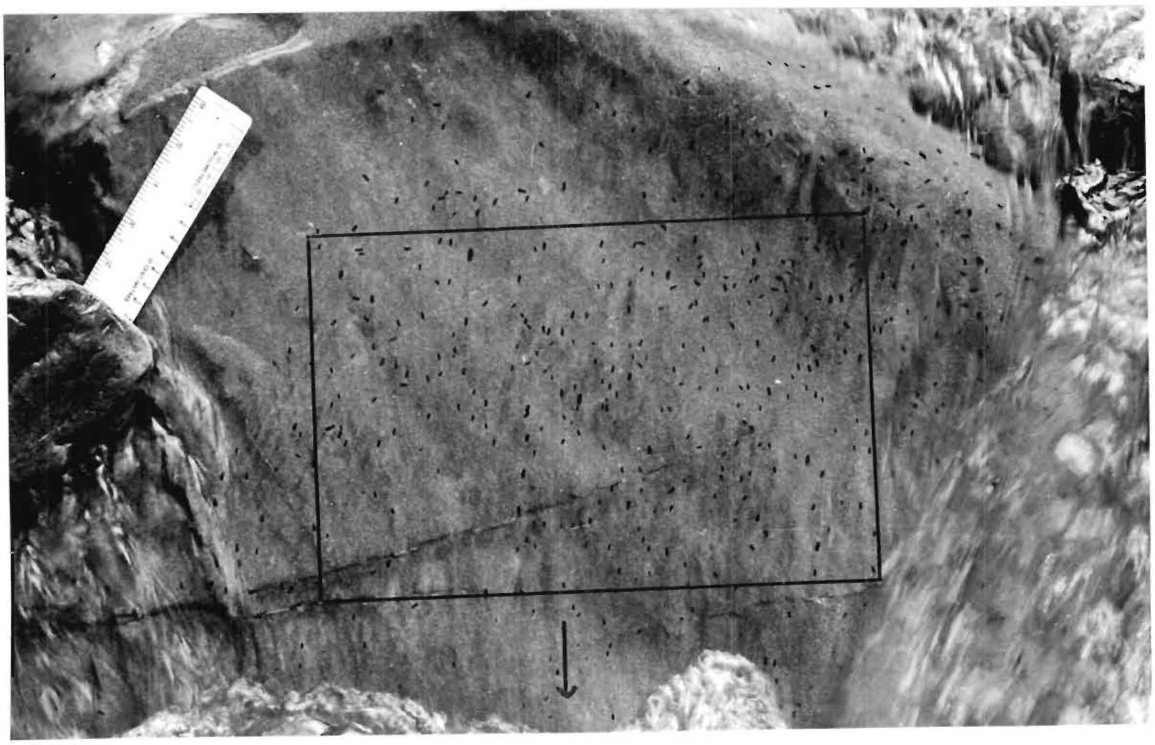
The rocks at Purau exhibit a great range in texture, but analysis of variance showed that there was no significant preference (p just greater than 0.05) by either larvae or pupae for any particular rock texture. They may however tend to prefer medium textured rocks.

Bealey Chasm:

It has been suggested previously (p.13) that floods may be one of the factors that determine overall larval distribution within the Bealey Chasm study area. However, water velocity and depth are probably more significant within areas generally suitable and their possible effects on larval distribution are considered below.

Vertical Populations: When the water runs swiftly past a rock or wells up against the upstream edge of a rock, the larvae are generally concentrated in a narrow band along the water level (Plate 5a). Larvae found in such positions are termed vertical populations. The number of larvae decreases with depth of water and it is rare to find larvae in more than 30 cm. of water. Plate 5b shows such a vertical population with the greatest concentration near the water level (middle left of photograph) and the fall off with depth (mid-bottom of photograph).

A series of samples taken at different depths from a vertical population of larvae similar to that in Plate 5a, showed not only a fall off in number but a change in the composition of the population with depth (Table 6).



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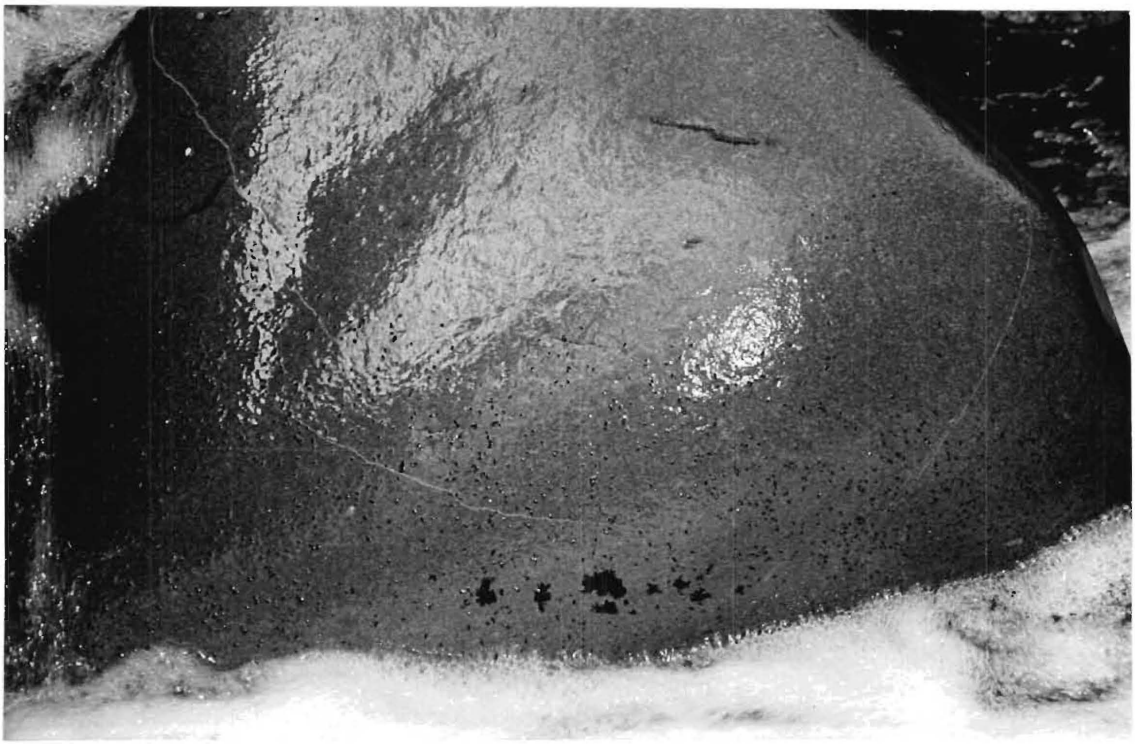


b

Table 6.

Distribution of larval instars in a vertical population. (July 1963) at Bealey Chasm.

Depth.	Instar Stage			
	First.	Second.	Third.	Fourth.
0-2 cm.	-	42	210	-
2-12 cm.	-	5	97	-
12-22 cm.	-	5	82	-
22-28 cm.	-	6	31	4

Length of rock swept = 20 cm.

Note: First instar larvae which are normally present in low numbers at this period of the year (Fig. 16) were not found in the above sample.

First instar larvae at Bealey Chasm, when present, are like those of N. chiltoni, grouped around the empty egg cases. At Bealey, however, they occur in the hygropetric zone as the adults do not crawl beneath the water surface to oviposition.

Horizontal Populations: These populations, which occur on rocks beneath an even flow of shallow (2-3 cm.) water (Plate 6a), are far more variable than the vertical populations (Table 8 , p. 60). In fact rocks which are close together in similar conditions can have widely differing compositions of larval instars. Larval distribution in the horizontal population depicted in Plate 6a was tested for randomness against the Poisson Distribution. The test showed that with grid sizes of 8 sq.cm. and 64 sq.cm., the distribution of the larvae was significantly different ($p < .005$) from a Poisson Distribution signifying that the larvae were clumped.

Hygropetric Larvae: In positions where the hygropetric zone is particularly extensive large numbers of larvae are often found some distance out of the water (Plate 6b). This distribution is restricted to the winter months; during the summer the hygropetric zone drys rapidly and is much reduced. The distribution of the larvae, apart from the more obvious larval aggregations (p.38) appears similar to that of the horizontal larval populations. Some species of Apistomyia and Philorus are normally hygropetric (Kitakami 1950, Gibo 1964).

Larval Aggregations.

As well as the aggregation of the first instar larvae and larvae in vertical populations, there occur at times, particularly at Bealey Chasm, extremely dense aggregations of closely applied larvae (Plate 6b). Kellogg (1903) mentions that certain American blepharocerid larvae form "patches" and Stuckenberg (pers.comm. 1964) has also observed similar larval aggregations, which he believes are due to larval selection of the most favourable environmental conditions. Observations made during the present study suggest another explanation. Firstly, N. chiltoni larvae of all stages, in the laboratory, will form aggregations even where conditions are apparently very even over considerable areas of the substrate (see Frontispiece). Secondly, aggregations shown in Plate 4b, although apparently associated with the water level, are grouped in an area of very even conditions where the rock was being wetted only by a continual spray of water.

Aggregations of N. chiltoni larvae build up when wandering larvae instead of exhibiting the avoidance reaction (p.42) when touched by other larvae, simply stop. It appears that the aggregation forms in response to a thigmotactic reaction. Thus it does not seem likely that the aggregations are associated with special or favourable conditions.

It is not known how long the aggregations remain in the field, but those of N. chiltoni, in the laboratory, have lasted for up to three days before dispersing. It may be noted that these groups were extremely difficult to disperse artificially.

Discussion.

Hora(1930) believed that there was a correlation between the size of larva and the water velocity tolerated, but the distribution of first instar larvae both at Purau and Bealey Chasm, appears to be primarily determined by adult oviposition behaviour and the tendency for the larvae to remain around the empty egg cases.

The distribution of second instar larvae in both study areas appears to indicate a small amount of dispersal from oviposition sites and also a certain amount of preference for hygropetric zone of the rocks.

Neither the size of rocks nor the texture have any major influence on the distribution of third, fourth or pupal instars of N. chiltoni and it was not possible to test the influence of water velocity beneath the rocks and in other positions inhabited by these stages.

The effects of rock size and texture on larval distribution at Bealey Chasm were not tested because the majority of rocks inhabited by larvae were deeply embedded and all were of a smooth texture.

The larval distribution in vertical populations at Bealey Chasm shows that there may indeed be a correlation between larval size and water velocity, for the smaller larval instars appear to prefer the slower surface water and the larger larvae the deeper swifter water. The more uniform distribution of larvae in the horizontal populations, which have a uniform water flow over

a wide area, also points to a velocity effect in vertical populations.

It is not considered that availability of food affects the distribution of larvae in areas otherwise suitable, as, in the clear water at Bealey Chasm, light penetration is good and algal growths can at times be seen to completely cover the submerged portions of the bed.

In horizontal populations, the larvae are clumped around the edges of relatively clear spaces. This could be due to larvae selecting the most favourable positions, but observations suggest that it is caused by larval avoidance reaction. This reaction in one larva initiates a similar response in the surrounding larvae leading to a general clearance from the centre of disturbance. The positions of clear regions on the rocks vary as the larval groups are continually forming and dispersing.

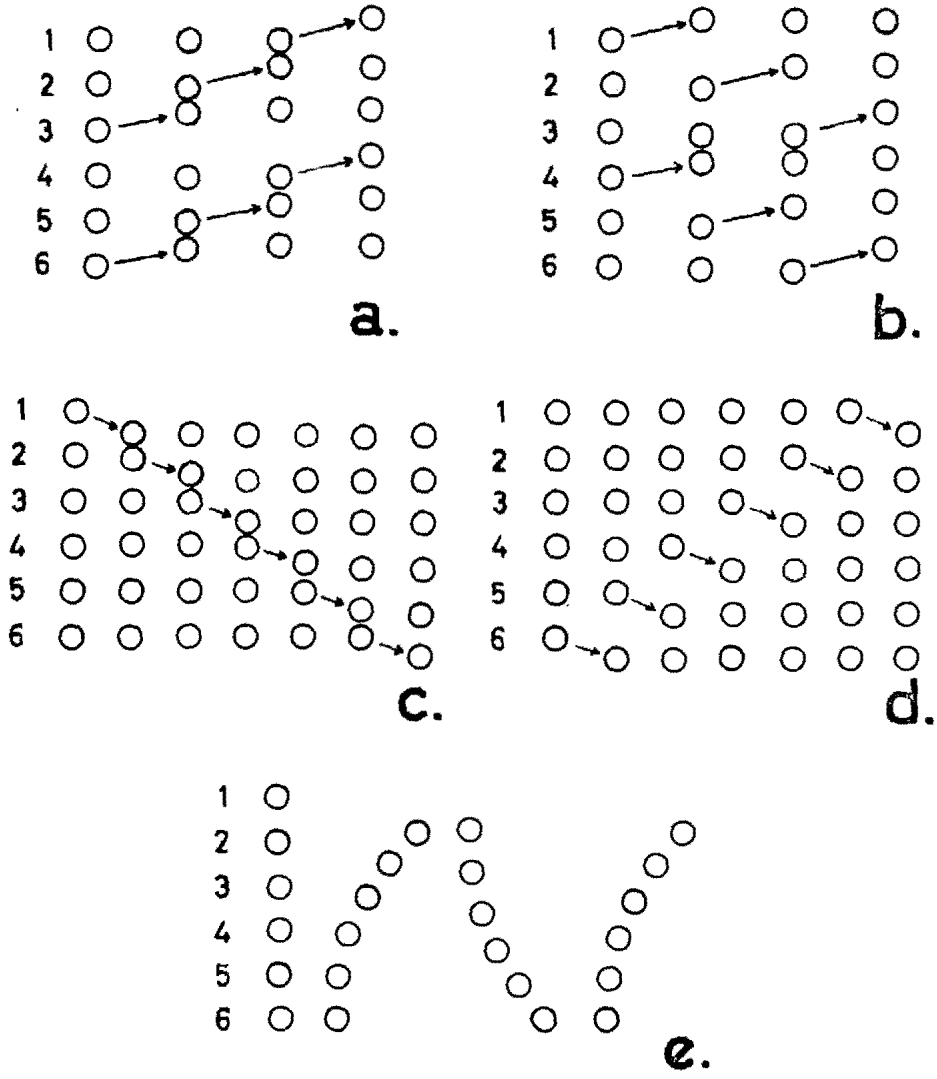

1
2
3
4
5
6
a.
b.
c.
d.
e.

FIGURE 4.

Larval sucker movement.
a. Forward movement in N. chiltoni.
b. Forward movement in L. cinerascens.
c. Backward movement in N. chiltoni.
d. Backward movement in L. cinerascens.
e. Sideways avoidance reaction in N. chiltoni.

Arrows indicate movement reaction in individual suckers. b and d derived from Dorier and Vaillant (1954).

Larval Movement.

Blepharocerid larvae observed in the three study areas and at other localities, when in swift flowing water, usually rest and feed with the body facing downstream (Plate 6a). Similar behaviour has been recorded for other blepharocerid larvae by Mannheims (1935) and Dorier and Vaillant (1954). Hora (1930), however, stated that blepharocerid larvae orientate themselves with the body at right angles to the water current and move with a sideways motion. There is some evidence, discussed later, that Hora's observations were made on disturbed larvae, for as far as is known there is no other reference in literature to blepharocerid larvae being normally orientated at right angles to the current.

Forward Movement: Laboratory observations on 4th instar larvae of Neocurupira chiltoni show that undisturbed larvae, move forward at 4.5-5.5 cm./min. During this forward locomotion, the suckers appear to move in two groups, the first of suckers 1, 2 and 3, and the second of suckers 4, 5 and 6. A wave of forward displacement of the suckers appears to pass anteriorly simultaneously in each group, so that suckers 3 and 6 move first then 2 and 5, and finally 1 and 4 (Fig. 4a). This pattern of sucker movement follows Hughes's rule (Wilson 1966) for insect locomotion in that "a wave of protraction (forward movement of the legs relative to the body) runs from posterior to anterior".

The above sequence was not always followed and more complex patterns were sometimes observed.

Dorier and Vaillant (1954), after studying the movement of Liponeura cinerascens, stated that movement of the suckers was as follows:- suckers 1 and 4, then 2 and 5, and finally 3 and 6. The wave of forward displacement of the suckers apparently passing posteriorly (Fig. 4c).

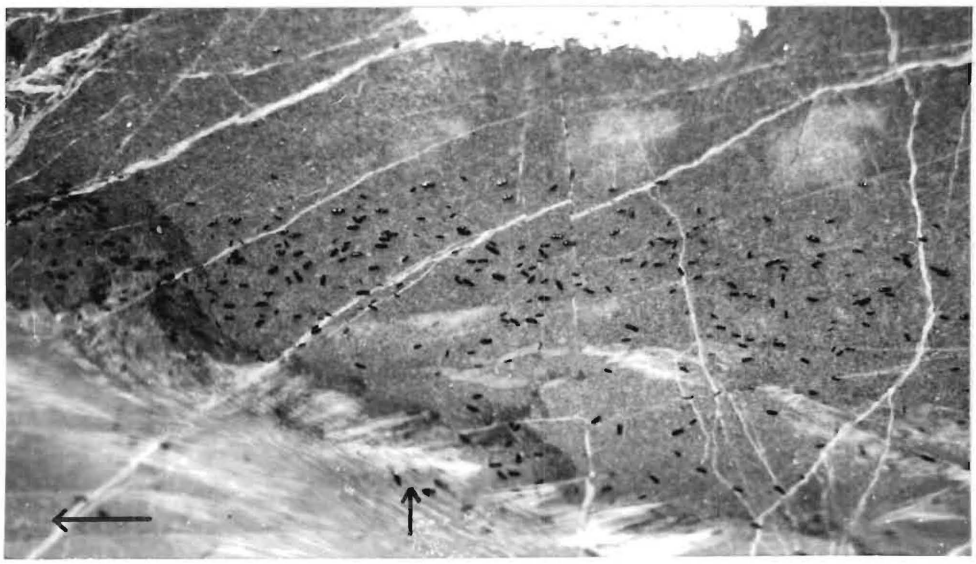
Tonnoir (1930) stated that the suckers of Peritheates intermedius moved forward one at a time starting from the anterior end. In general similar to L. cinerascens.

Backward movement: When N. chiltoni larvae in the artificial stream were in such a position that required backing away, a wave of sucker displacement, starting with the first sucker, was passed posteriorly down the body (Fig. 4c). During this movement only one sucker was moved at a time and progress was consequently slower than in forward movement. Only 4-5 cycles of sucker displacementwere carried out at one time, the larvae then swung sideways and attempted to continue normal forward movement.

Dorier and Vaillant (1954) investigated backing of Liponeura cinerascens also, but reported that the wave of sucker displacement starts with the sixth sucker and travels forward (Fig. 4d).

Sideways Avoidance Reaction: When blepharocerid larvae in the artificial stream or in the field were disturbed either by removal from the water or by touching the body, in particular the antennae, they reacted violently in a characteristic manner. The 4 anterior suckers are released and the anterior portion of the body is swung to either side as far as possible and re-attached to the substrate. The 4 posterior suckers are then released and the posterior portion of the body swung the same direction as the anterior (Fig. 4e). This series of movements is only repeated 3-4 times and the larva continues with a rapid normal forward movement.

The sideways avoidance reaction is very rapid and a 4th instar N. chiltoni larvae can move up to 24 cm./min. for the short time it is continued.



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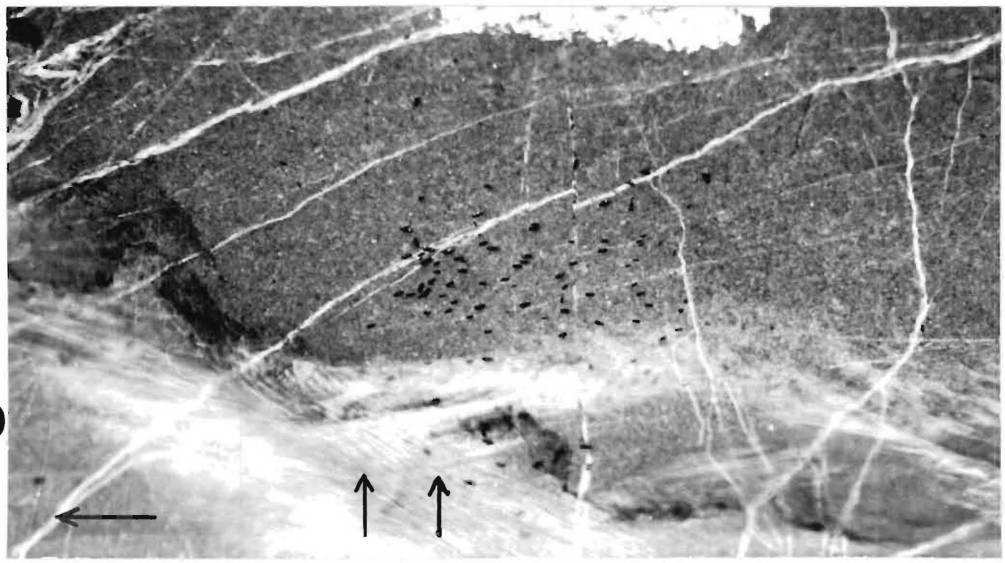


b

c

Dorier and Vaillant (1954) stated that, after exhibiting the avoidance reaction, larvae of Liponeura cinerascens moved upstream using the normal forward motion. New Zealand blepharocerids in swift water, on the other hand move downstream after this reaction.

To illustrate this, a reference mark 8 cm. long was made on the water line of a rock that was populated with second and third instar N. campbelli larvae (Plate 7a). The larvae below and then above the reference mark were removed (Plate 7b) and this disturbance caused those remaining to respond with the avoidance reaction and move downstream. In the few seconds that it took to remove the larvae and take a photograph (Plate 7b) the remaining larvae had already moved approximately 1 cm. Within five minutes most had moved downstream, with the greatest distance travelled approximately 6 cm. (Plate 7c), and the larvae above those removed had moved downstream to approximately the reference mark. Observations were continued for three more hours, but little further movement was noticed.

If the sideways avoidance reaction is common to all blepharocerid larvae, as is probable, then it is possible that Hora's observations on the orientation and movement of blepharocerid larvae as well as the observation on sideways movement made by Edwards (1929) were made on disturbed specimens. A suggestion strengthened by Tonnoir's (1930) statement that blepharocerid larvae do not move sideways unless disturbed.

The discrepancies in the observed patterns of sucker movement, during the forward and the easily observed backward locomotion in N. chiltoni, L. cinerascens and P. intermedius, may not be fully resolved at the present as they probably result from differing interpretations. It is possible, however, that there is a real difference in the sucker movement during locomotion, at least between N. chiltoni and L. cinerascens.

Death Mimicry.

When blepharocerid larvae are shifted from fast flowing water to still water, the three anterior suckers are lifted off the substrate and the anterior end of the body is arched backwards. This position alternates with short periods of rapid forward motion. When the larva dies, in such conditions or is killed with alcohol, the body is arched with the suckers on the convex surface.

A similar attitude is taken up by larvae dislodged from the substrate. Kitakami (1931) originally commented on this behaviour of dislodged larvae, which he termed "death mimicry".

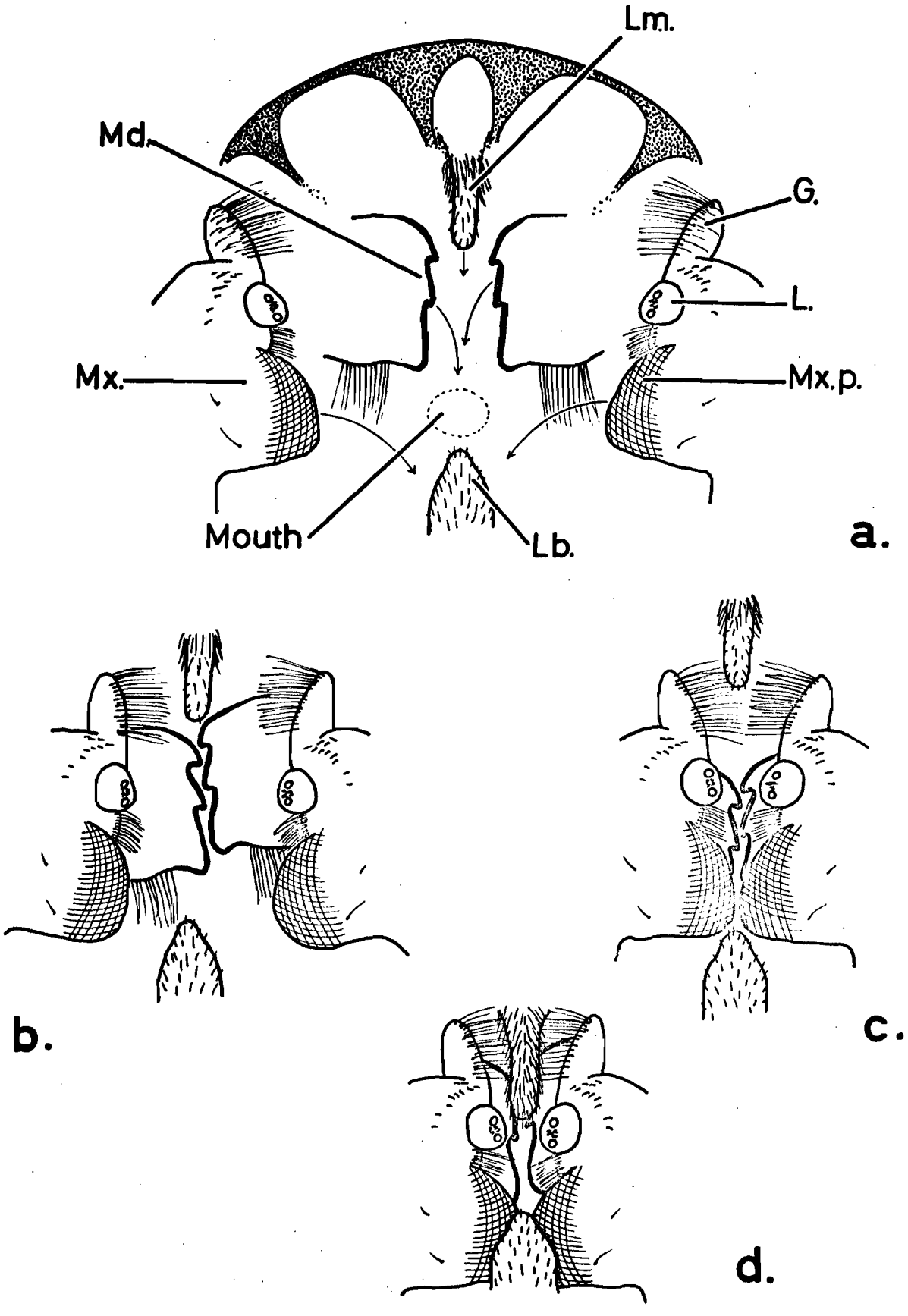
Observations in the laboratory and field show that larvae in this attitude are carried downstream with the suckers foremost and as soon as any of the suckers touch a solid object, attachment occurs. This attitude is therefore of great importance for survival, as the dislodged larva will only survive if it reattaches as soon as possible in a swiftly flowing portion of the stream and is not deposited in a slowly flowing pool.

Larval Feeding.

Blepharocerid larvae graze on the algal layer covering the rocks on which they live.

Mouth parts: The larval mouth parts are anteroventrally orientated and form a cone shaped mass pointing towards the substrate. Anteriorly they are bordered by the heavily chitinised frons and lateralia. Strong internal projections from these head sclerites provide attachments for the mandibles and maxillae.

Laboratory observations on the feeding of N. chiltoni larvae show that the mouthparts when opened are arranged as seen in Fig. 5a. The labrum is a rather deep narrow structure with a covering of stout hairs. Each mandible is thick and heavily chitinised with three serrations on the leading edge and a group of long stout


Lm.
Md.
G.
L.
Mx.
Mx.p.
Mouth
Lb.
a.
b.
c.
d.

hairs on the posterior edge. The interpretation of the maxilla, as used here, is shown in detail in Appendix III (Fig. 2). The main features of the maxilla are the cushion-like maxillary palp covered with rows of small pectinate hairs, the sensory lacinia and the galea covered with stout hairs. The mouth is located directly anterior to the labium which is a cone -shaped structure covered with fine stiff hairs.

The mandibles move together, one slightly ahead of the other, while scraping the substrate in a medio-posterior direction. They appear to touch just anterior to the mouth (Fig. 5b), and more posteriorly as a unit to cover the mouth. The maxillae move similarly to, but later than the mandibles, and also scrape food from the substrate (Fig. 5b & c). As the mandibles begin to move anteriorly, the maxillae move further posteriorly and the maxillary palpi slip under the labium (Fig. 5d). As the mandibles move anteriorly the mandibular hairs may possibly sweep food particles into the mouth. While the labium is sweeping the maxillary palpi the labrum appears to move posteriorly and sweep the hairs on the two galeae. After the maxillae have been swept by the labrum and labium their return stroke is rapid. At this stage the mandibles having returned to their original position begin a new medio-posterior stroke.

It is considered that the main food collecting device is the maxilla. The maxillary palpi with their rows of fine pectinate hairs are well adapted to scrape small algal particles from the substrate. Whereas, the mandibles appear singularly ill-adapted for this role. Tonnoir (1930) reached a similar conclusion, while Bischoff (1928) and Wesenberg-Lund (1943) believed the maxillae acted as filters.

Observations do not support Kellogg's (1902) inference that the larvae eat the epizooic algae from their own dorsal surface or from other larvae.

It is of sufficient interest to record that Ephemeroptera larvae in the artificial stream kept N. chiltoni free from algal growths after they had consumed the algae on the stones and walls.

Food: In the laboratory larvae preferred thin layers of algae and did not select particular algal species.

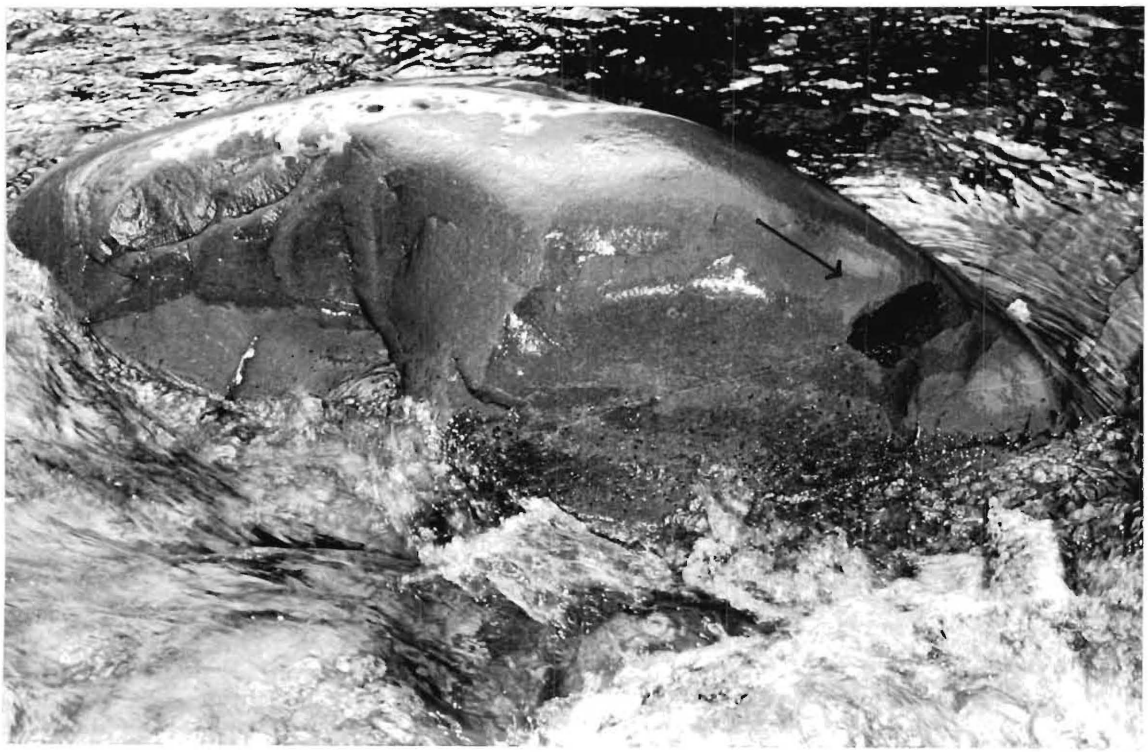
They would not eat algae with a thickness greater than 0.5-1.0 mm. and tended to remain in areas free from heavy algal growths. This resulted in small patches of rock being kept clear of algae. Similar patches have been observed on the rocks at Purau during the summer when algal growth is heavy. Either the larvae are unable to feed off the thick algae or this behaviour is a consequence of their inability to attach to a soft substrate. N.chiltoni larvae moving from colonies of Melosira to colonies of Oscillatoria while feeding, produced faecal strings showing algal bands corresponding to the algal colonies traversed during feeding. Colour changes in the Melosira indicated that some digestion had occurred, but Oscillatoria retained its original colour and was still capable of movement. This suggests that the larvae were not selecting algae for their nutritive value.

Prepupal Behaviour.

Blepharocerid prepupae actively search for suitable pupation sites.

The pupae of Neocurupira chiltoni are usually found in depressions on the undersides of stones. There appears to be little orientation to the current at Purau, This may be be due to the lower current regime there, for N. chiltoni prepupae in the laboratory orientate themselves with the anterior end downstream. N. chiltoni prepupae do not form aggregations similar to those of the blepharocerid prepupae at Bealey Chasm.

a



b

At Bealey Chasm the prepupae of some species select pupation sites which are used each season. These sites are in places such as the downstream side of a large rock just out of the main water flow, or in crevices in the rock where the water current is reduced. Large pupal aggregations are usually present in these sites by the end of the summer (Plate 8).

Similar blepharocerid pupal aggregations have been mentioned and figured by Mannheims (1935), Wesenberg-Lund (1943) and Gibo (1964).

In the pupal aggregations at Bealey Chasm the pupae are normally all aligned with the water current in the same way as N. chiltoni in the laboratory i.e. they have their anterior ends facing downstream. Similar behaviour was noted by Mannheims (1935) but Stuckenberg (1958) stated that Pauliana umbra pupates facing upstream.

The pupal aggregations at Bealey Chasm contained the pupae of N. campbelli and P. turrifer. Very rarely were pupae of N. hudsoni found in these positions. The absence of N. hudsoni was surprising as 4th instar larvae of this species were quite common at times, in the same places as the larvae of the other two species. This strongly suggests that N. hudsoni prepupae prior to pupating have different behaviour to that of N. campbelli and P. turrifer. Aggregations of N. hudsoni pupae were never found in readily accessible situations and the character of Bealey Chasm made the search for pupae at deeper levels dangerous.

Pupal Development.

Laboratory observations on the pupation of Neocurupira chiltoni agree closely with the detailed accounts given by Tonnoir (1930) and Mannheims (1935) of the pupation of Peritheates intermedius and Liponeura belgica respectively.

Because the pupation of blepharocerids usually occurs in swiftly flowing water, it has been suggested by Dumbleton (1963a) and others that the ventral larval skin is retained to provide continuous attachment during the process of pupation. But laboratory observations on the pupation of N. chiltoni, as well as the descriptions by Tonnoir and Mannheims, show that the complete larval skin including the suckers is sloughed off during pupation. The suckers, however, even though they have been detached from their internal musculature and are moved posteriorly with the rest of cuticle, are capable of maintaining an attachment to the substrate until the pupal cement hardens. This apparently passive functioning of the sucker also suggests that the attachment in the blepharocerids is due to shape and physical factors as suggested previously (p. 16).

Laboratory records show that the time taken for the pupation of N. chiltoni varied from 8-10 minutes and that the development of the adult took from 29-37 days at temperatures ranging from 7°-14°C. Insufficient larvae pupated in the artificial stream to determine the relationship between rate of development and temperature.

Tonnoir (1930) found that P. intermedius took 5 minutes to pupate and Mannheims (1935) stated that the pupal stage occupied from 23-27 days.

Emergence of the Adult.

Pre-emergence behaviour was observed in Neocurupira chiltoni pupae that had pupated on the perspex sides of an artificial stream.

The fluid filled spaces between the adult and the pupal case became gas filled approximately three days before adult emergence (See Frontispiece). The origin of the gas is unknown.

Emergence of N. chiltoni adults and other New Zealand blepharocerids is by the normal orthorrhaphous method and is very similar to the emergence of Blepharocera fasciata (described and figured by Mannheims 1935). The adult emerges through a T-shaped split along a preformed line of weakness in the prothoracic and mesothoracic sclerites. Although adult emergence was not observed in the field, laboratory observations on emerging N. chiltoni adults show that a normal emergence, with the adult working itself free by alternate lateral movements, takes approximately 5 minutes. One adult, however, took approximately 24 hours to complete the process due to leg entanglement with the pupal case. This normal emergence time agrees with the 3-5 minutes for emergence given by Alexander (1963). Mannheims (1935), however, states that Liponeura belgica took from 15 minutes to 1 hour, again depending on the difficulty encountered in disengaging the long legs from the pupal case. Gibo (1964) reported that Philorus yosemite took approximately 13 minutes to emerge.

Mannheims suggested that the orientation of blepharocerid pupae in fast flowing water (p.47) was an adaptation which allowed the water current to assist the adult to emerge. But the pupal orientation (Stuckenberg 1958) of Paulianina umbra indicates that current may not be important in adult emergence.

It was observed in the laboratory that the bubble of gas that surrounded the adult in the pupa prior to emergence remains with it during emergence and is partially responsible for its rapid movement to the water surface.

Because the wings are fully expanded in the pupa (common to all blepharocerids), the N. chiltoni adults flew immediately on reaching the water surface.

Observations by Kellogg (1903), Wesenberg-Lund (1943) and Alexander (1963) suggest that emergence of the adult is hazardous for they perish if swept away. Present observations on adult emergence, avoidance reaction (p.51), oviposition behaviour (p.56) and an examination of the adult cuticles (below), suggest that the adults if swept away are not troubled by wetting, and are capable of flight as soon as they reach the water surface.

Hydrophobic Nature of the Adult Body.

The wings of all described New Zealand blepharocerids (Chpt. I) are covered with microtrichia.

Sections of the abdomen and thorax of N. campbelli, N. chiltoni and N. hudsoni adults show a dense layer of very fine hair, .002 mm. long with curved tips, over the abdomen. Those covering the thorax are .005 mm. long and are not curved at the tips. In Hapalothrix lugubris (supplied by B.M. Mannheims) the abdominal hairs are longer - .003 mm. and sparser than those of the Neocurupira spp. Those covering the thorax are .007 mm. long.

The abdominal hair covering in these species is very similar to that described by Thorpe and Crisp (1949) in the plastron respiration of certain aquatic Coleoptera. However, the large bubble of air that surrounds adults during periods of submergence (emergence, oviposition and avoidance reaction) indicates that the hair layer does not act as a true plastron, but rather enables the adult to carry a sufficient air store while submerged, and prevents wetting.

The non-wettability of blepharocerid adults has been commented upon by Mannheims (1935) and Alexander (1963).

Flight.

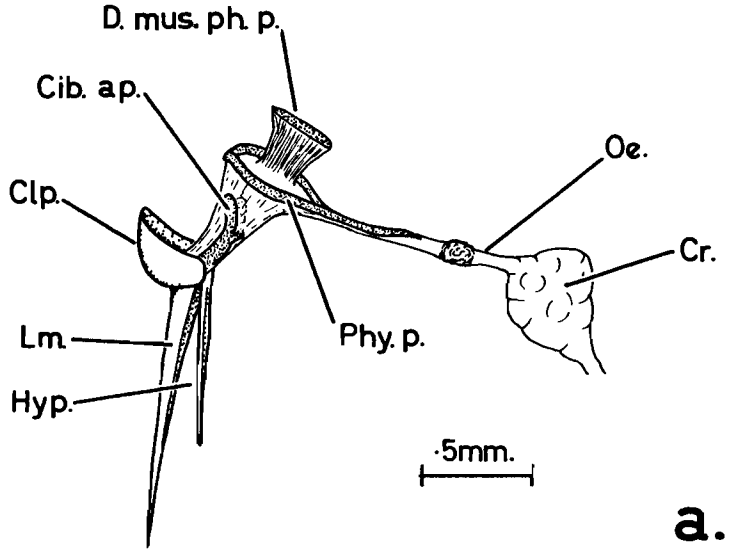
Normal: In the New Zealand species so far observed both sexes generally fly low over the white foaming water below a rapid or cascade. The adults of N. campbelli and N. chiltoni are found more frequently than other species flying along the waters edge in quieter stretches.

During flight the fore-legs are held high in front of the thorax while the hind-legs are trailed behind the abdomen. In the laboratory, N. chiltoni females were observed to hold their fore-legs back over the thorax, but this behaviour was never observed in the field.

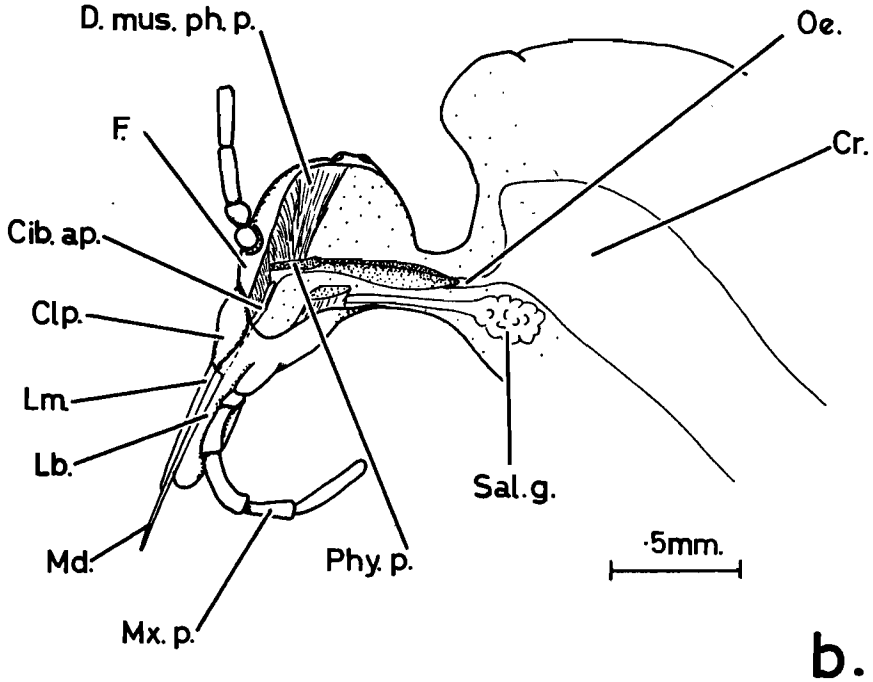
Most adults seen resting, with the exception of N. campbelli, were on the hygropetric zone of rocks in rapids. Few were found on dry rocks. N. campbelli on the other hand, is found more commonly on the underneath surface of rocks that closely overhang the water of quieter pools below rapids and cascades. All known New Zealand species of blepharocerid adults rest with the legs outstretched and the wings at right angles to the body and parallel to the substrate.

Avoidance Reaction: New Zealand blepharocerid adults when disturbed (by other adults, gusts of wind or collecting nets) drop or actively fly into the water, which carries them away. However, adults very quickly reappear following the disturbance.

Adults are not damaged even when swept into foaming water and are not caught in the surface film, so that they immediately fly on re-emergence.


D. mus. ph. p.
Cib. ap.
Clp.
Lm.
Hyp.
Oe.
Cr.
Phy. p.
·5mm.

a.


D. mus. ph. p.
F.
Cib. ap.
Clp.
Lm.
Lb.
Md.
Mx. p.
Phy. p.
Oe.
Cr.
Sal. g.
·5mm.

b.

Feeding of the Adult.

It is known that some blepharocerid females which possess mandibles are predaceous on other insect adults (mainly dipterans) and are at times cannibalistic (Mannheims, 1935 , Kellogg 1903 , Pryor 1948 and Downes 1958a). The males as well as the mandibulate females of these species and both sexes of the nonmandibulate species have been recorded drinking nectar from various flowers. (Kellogg 1900, Hetscko 1912, Mannheims 1935, and Alexander 1963).

None of the known New Zealand species of blepharocerid possess mandibles. Although the galea is well developed in some species (Chpt. I) and could perhaps act as a mandible, no adults have been observed preying on blepharocerids or other insects.

The presence of pseudotracheae on the distal ends of the labial palpi of all known New Zealand species, with the exception of N. campbelli, suggested to Dumbleton (1963a) that the adults may feed on flower nectar.

In an attempt to discover what food New Zealand blepharocerid adults might be capable of eating, the anatomy of the dissected and sectioned anterior alimentary canals of Neocurupira chiltoni and N. hudonsi ~~were~~ was compared with that of Liponeura cinerascens (a known predator). Unfortunately no specimens of known nectar feeding blepharocerids were obtainable for comparison.

Cibarial Pump: The retractor muscles running from the cibarial apparatus (pump) to the frons in L. cinerascens (Fig. 6b), and common in predaceous culicids (Clements 1963), were apparently absent in the N. hudsoni specimens examined (Fig. 6a). They were present in N. chiltoni, but were much smaller than in L. cinerascens. All species examined possessed well developed dilator muscles passing from the cibarial apparatus to the clypeus.

Pharyngeal pump: All the pharyngeal pumps were of a similar robust build, but that of L. cinerascens had the greatest depth of the chitinous oesophageal extention.

Oesophagus: The thickening of the oesophagus, present in N. hudsoni, was not apparent in L. cinerascens.

Crop: The crops of N. hudsoni and N. chiltoni, appeared as small folded distentions of the gut, while the crop of L. cinerascens was much larger and occupied a considerable part of the thorax.

Salivary Glands: Salivary glands which were prominent in L. cinerascens were not found in the other species examined.

The lack of mandibles, salivary glands and the small crop size, suggests that N. chiltoni, N. hudonsi, and hence perhaps other New Zealand blepharocerids are not predators. On the other hand the presence of a well developed pharyngeal pump and pseudotrachea on the labial palpi, suggest, as already suggested by Dumbleton (1963a), that New Zealand blepharocerids feed on flower nectar.

Nectar-bearing plants were searched regularly during this study, but only one adult was ever collected from them. This was an N. hudsoni male, and examination showed that it had not been feeding.

N. chiltoni males showed no interest in various nectar-like solutions in the laboratory.

In the laboratory and field, blepharocerid adults have been observed placing their mouthparts on wet rocks and apparently taking up water. Mannheims (1935) reported similar behaviour for Hapalothrix lugubris which also lacks mandibles.

This present study suggests then that some New Zealand blepharocerid adults do not feed but at times take up water.

Mating.

Searching: As males do not appear to feed, most flight is probably in search of females.

The males often fly in loose swarms of a dozen or more individuals. The swarms will maintain a constant position over a foaming portion of the stream for a few minutes and then either disperse or shift to another position. This appears to be true swarming in the sense that Downes (1958b) used the term and is not just a natural abundance of the adults. The swarms, usually composed entirely of males, may settle for short periods.

When not swarming the males fly along the waters edge as previously described (p.51). Females tend to remain on the rocks, but occasionally fly along the waters edge also.

A male making contact with a resting adult normally results in either: -

(a) If the resting adult is a male or a non-virgin female, the other is rejected by a flick of the wings or legs. If the resting adult is badly disturbed by the contact it will either fly off or respond by avoidance reaction.

(b) If the resting adult is a virgin female no rejection takes place and copulation follows.

Downes (1958b) reported that mechanical stimulation of the legs in the culicid Culiseta inornata will elict a mating response. Stimulation of the legs of N. chiltoni females with fibres produced no observable response. This may be because female blepharocerids in contrast to female culicids, have a passive role in copulation.

Female blepharocerids are normally in short supply (p.67). This results in, intense competition among males, and as Mannheims (1935) has also observed, in newly emerged females, still soft and pale, being found in the midst of a fighting mass of males.

Copulation: Mannheims (1935) has described and figured the copulation position of Liponeura belgica and as far as is known all New Zealand blepharocerids copulate in a similar manner.

According to Downes (1958b), the Simuliidae show a correlation between eye structure and copulation locality. He found that simuliids with simple eyes copulate on the ground, while those with divided eyes copulate in flight.

As far as can be gathered there is no such correlation in the Blepharoceridae. For according to Dumbleton (1963a) Edwardsina australiensis (simple eyes) copulates on the ground as do all known New Zealand blepharocerids (divided eyes), and Hapalothix lugubris (divided eyes) and most Liponeura spp. (simple eyes) copulate in flight while L. vogesiaca (simple eyes) copulates on the ground (Mannheims 1935).

At Bealey Chasm Peritheates turrifer adults have been timed copulating from 30 sec. - 35 minutes before being disturbed by other adults, while according to Mannheims, Humbault timed the copulation of L. vogesiaca for at least 15 minutes.

Oviposition.

Female blepharocerids emerge from the pupa containing eggs already well developed. Dissection of pharate females and newly emerged females of Neocurupira campbelli and N. chiltoni, shows that they contain between 54-116 and 82-269 eggs respectively. However, one exceptionally large N. chiltoni female laid 336 eggs in the laboratory.

Although not tested, egg number in the female is probably correlated with body size.

It seems probable that in New Zealand blepharocerids feeding is not necessary for the maturation of the eggs. In this, blepharocerids differ from those Nematocera which require food before the eggs mature.

Observations in the field and in the laboratory show that in N. chiltoni oviposition immediately follows copulation. It appears that all the eggs are laid at one time, for dissection of laboratory reared females after a single oviposition attempt showed them to be empty of eggs. This suggestion is supported by large numbers of eggs, at the same stage of development, being found in patches on rocks in the field.

Mannheims (1935) described and figured for Liponeura belgica a similar method of oviposition to that observed in most New Zealand blepharocerids. Neocurupira campbelli, N. hudsoni and Peritheates turrifer oviposition in small depressions in the rock in the hygropetric zone, while N. chiltoni females normally crawl down the rock and oviposition in similar depressions below the water level.

While ovipositing underwater, the female is surrounded by a layer of air, but remains attached to the rock in spite of the high buoyancy and the water velocity.

Most female adults after oviposition reject further copulation attempts by males and remain resting on the rocks. Others, however, can be found flying with the males along the waters edge. Because New Zealand blepharocerid adults copulate on the rocks in the hygropetric zone and the females normally oviposite on the same rocks, the presence of blepharocerids in the Tributary to the Pu-Pu Spring River (p. 6) where there are no protruding rocks is unusual.

Longevity of Adults.

Mannheims (1935), Kitakami (1950) and Alexander (1963) stated that blepharocerid females live considerably longer than the males. Mannheims gave the length of life of blepharocerid males as three days, provided water was available.

During the present study N. chiltoni adults were raised in the laboratory. In these circumstances the males generally lived longer than the females (Table 7).

Table 7.

Longevity of N. chiltoni adults in laboratory conditions.

Longevity in days.	Number of Adults Raised.	
	♂	♀
3	1	4
4	-	2
5	2	-
6	1	-
7	2	-
8	-	1
Total	6	7
Mean length of life.	5.5	4.0

The difference in longevity between male and female is not statistically significant at the .05 level.

However, observations in the field also suggest that female N. chiltoni have a shorter life span than the male, for in collections, females which had already ovipositioned had torn wings and were apparently exhausted. Such females when brought back to the laboratory did not survive long in comparison with males collected at the same time.

This suggests that the imbalance of the sexes (large number of males and few females), in the collections taken from Purau and Kaituna, although basically a result of an uneven sex ratio in the pupae (p.67) and the different behaviour of the sexes is exaggerated by the short female life span.

The longevity of adult blepharocerids at Bealey Chasm was not considered as insufficient data ~~was~~ were available.

PART V. LIFE CYCLES.

The life cycles were investigated by the regular sampling of larval, pupal and adult populations.

Sampling.

Purau and Kaituna.

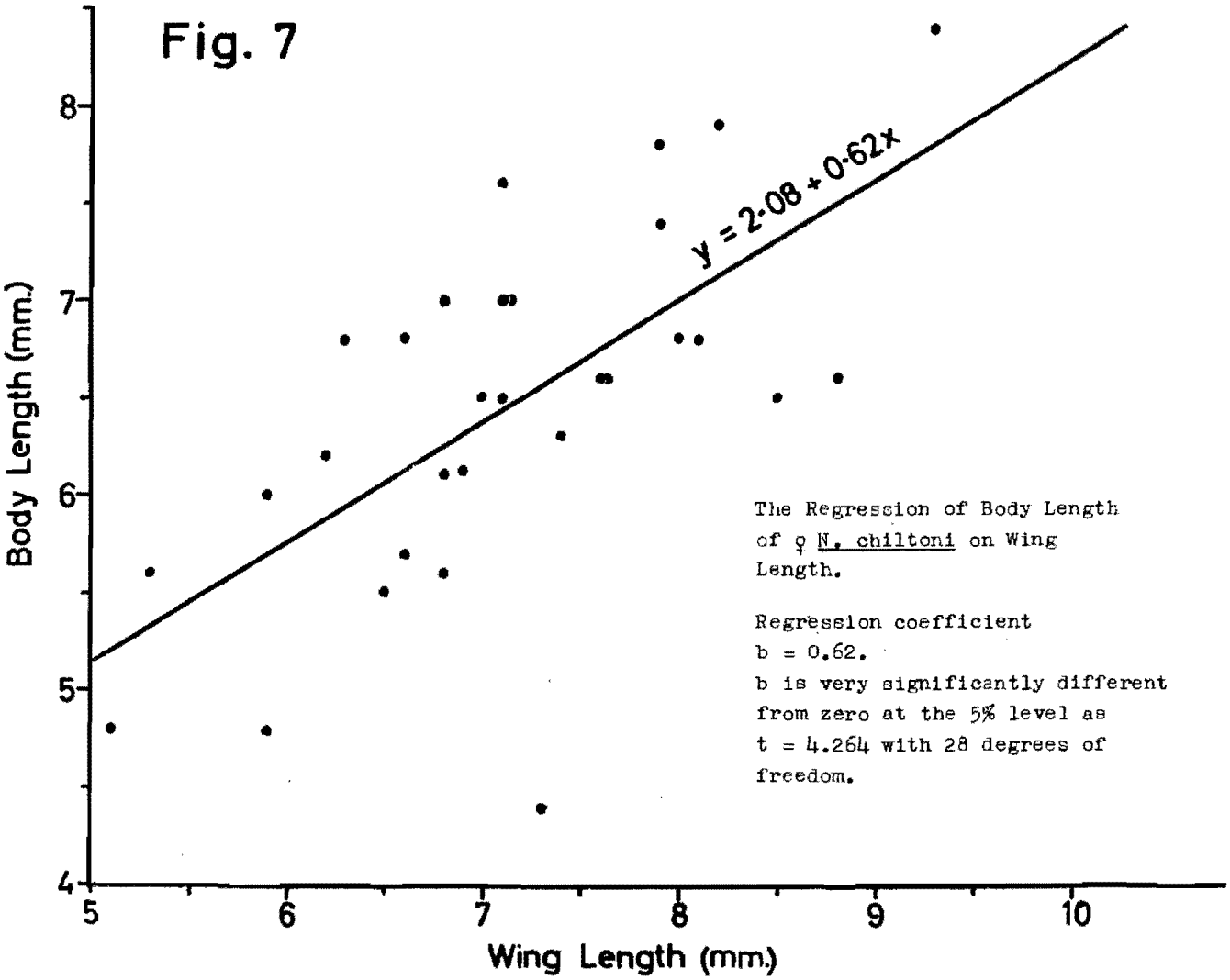
Larvae and Pupae: A technique similar to that used by Percival and Whitehead (1929) and Macan (1958) for sampling rocky streams, was used at both Purau and Kaituna.

Five medium textured rocks, not protruding above the water level, and each approximately 30 x 20 cm. in size were lifted from the water and the fourth instar larvae and pupae removed by hand.

(It was originally believed that the third instar larvae were unevenly distributed, as are the first and second instars, and that collections of this instar would give a poor indication of their abundance. However, later during the study a reconsideration of the larval distribution data (p. 35) indicated that the third instar larvae were as evenly distributed as the pupae.)

To test whether the samples were representative of the population in the study area, two separate samples were taken during the same collecting visit to Purau (App. 5). More samples were not taken as the effect of heavy sampling on the study area population was not known.

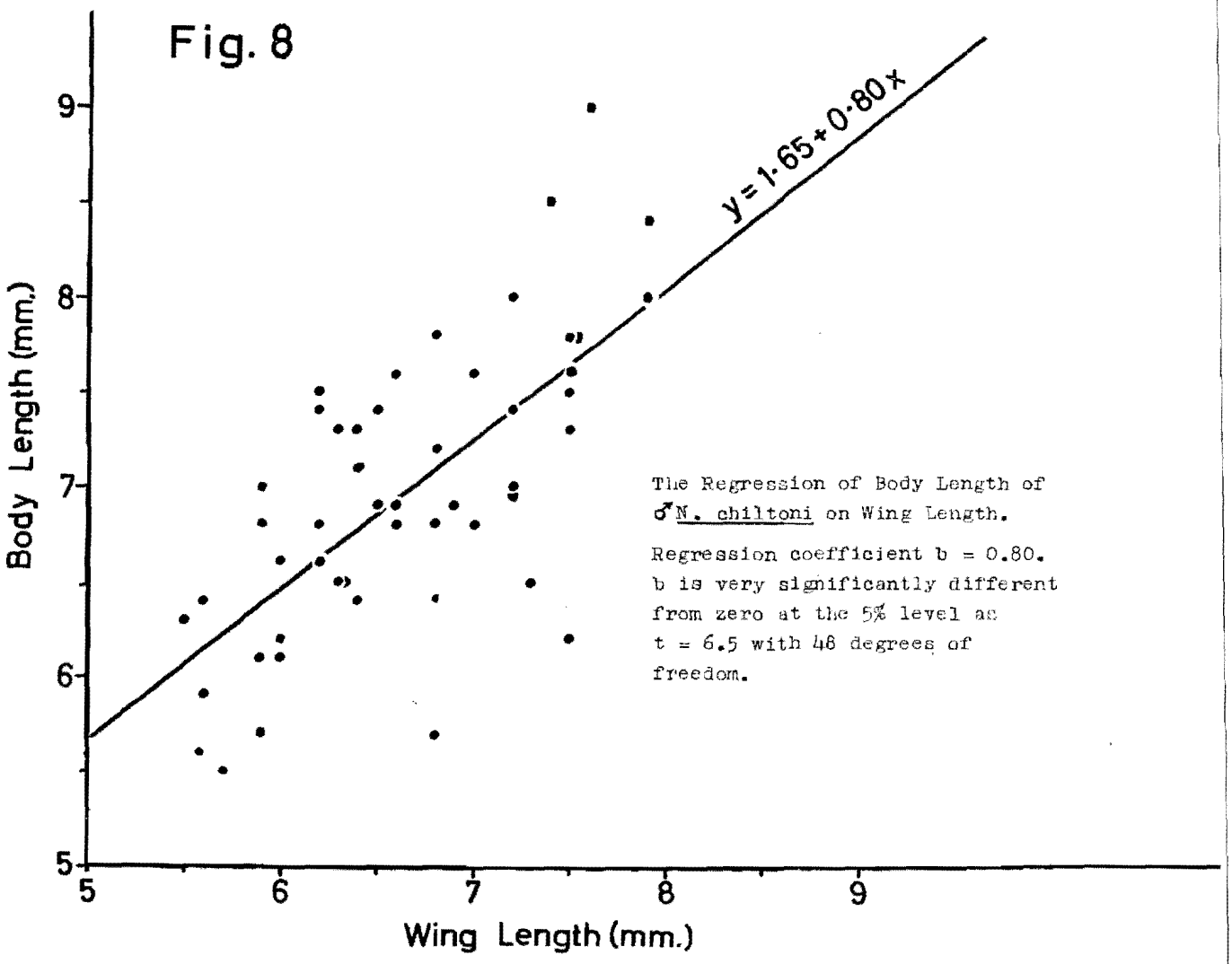
Fig. 7



The Regression of Body Length of ♀ N. chiltoni on Wing Length.

Regression coefficient
b = 0.62.
b is very significantly different from zero at the 5% level as t = 4.264 with 28 degrees of freedom.

Fig. 8



The Regression of Body Length of ♂*N. chiltoni* on Wing Length.

Regression coefficient b = 0.80. b is very significantly different from zero at the 5% level as t = 6.5 with 48 degrees of freedom.

The pupal:larval ratios and the mean pupal lengths of the two samples were not significantly different, but the mean larval lengths were significantly different ($.05>p>.02$).

Even though the mean larval lengths differed in the two samples, the mean larval lengths generally follow the seasonal changes of the mean pupal and mean adult wing length (Figs. 11 and 12). The test, though only on two samples, indicates that the sampling technique used gives data that is representative of the population and that the major differences in the pupal:larval ratio and mean pupal length have some significance.

Adults: The first two collections of adults were made by catching resting adults with tweezers. With this method many adults were missed as a result of the avoidance reaction.

Later collections were made with a large entomological net. This was swept up the stream with the lower rim of the opening just below the water level. In this way the adults flying, as well as those in the water following the avoidance reaction, were caught. Most male adults could be taken in a single sweep up the stream. However, sweeping failed to collect ovipositioning females which were normally under the water and did not release their hold of the substrate even when disturbed.*

Table 8.

Data for testing larval sampling technique at Bealey Chasm.

(a) Horizontal populations.

	Sample 1.				Sample 2.			
Instar.	4	3	2	1	4	3	2	1
N. campbelli.	3	42	13	4	-	7	17	4
N. hudsoni.	11	49	30		11	36	44	
P. turrifer.	-	-	-		-	1	-	
Total.	152				120			

(b) Vertical populations.

June.

	Sample 1.				Sample 2.			
Instar.	4	3	2	1	4	3	2	1
N. campbelli.	1	24	41	41	4	13	26	30
N. hudsoni.	3	14	82		-	24	76	
P. turrifer.	-	1	1		-	2	-	
Total.	208				166			

August.

N. campbelli.	-	41	60	99	-	21	59	93
N. hudsoni.	-	31	104		-	58	193	
P. turrifer.	-	5	-		-	3	-	
Total	339				427			

June and in August (Table 8b).

For the purposes of Chi-squared testing the ratios of the various instars present in the samples, the numbers of the fourth instar larvae were included in with the third instar larvae. In both sets of samples, there was no significant variation in the ratio of the total third and fourth instar larvae to the second instar larvae for either N. campbelli or N. hudsoni.

However, while there was no significant difference between the proportions of first instar larvae in the June samples, there was a significant difference between the August samples. This may have been caused by sample 1 having been taken from a more favoured oviposition site than was sample 2. The small number of fourth instar larvae within these collections prevents their mean lengths from being tested.

Pupae: The pupal aggregations were sampled separately from the larval populations. Pupae were dislodged from the rock with a knife and caught in a net placed downstream. As the aggregations were in relatively inaccessible situations, sampling was usually difficult and impossible during high water conditions. Because of the difficulty in obtaining samples from pupal aggregations, it is not possible to check whether the samples taken were representative of the pupal populations. Pupae collected were measured and if possible sexed.

Adults: Adults were collected by sweeping for a standard period of approximately 10 minutes; not all parts of the study area could be reached with the collecting net, so that the figures given are of relative abundance (Figs. 14, 15 and 16).

Fig. 9

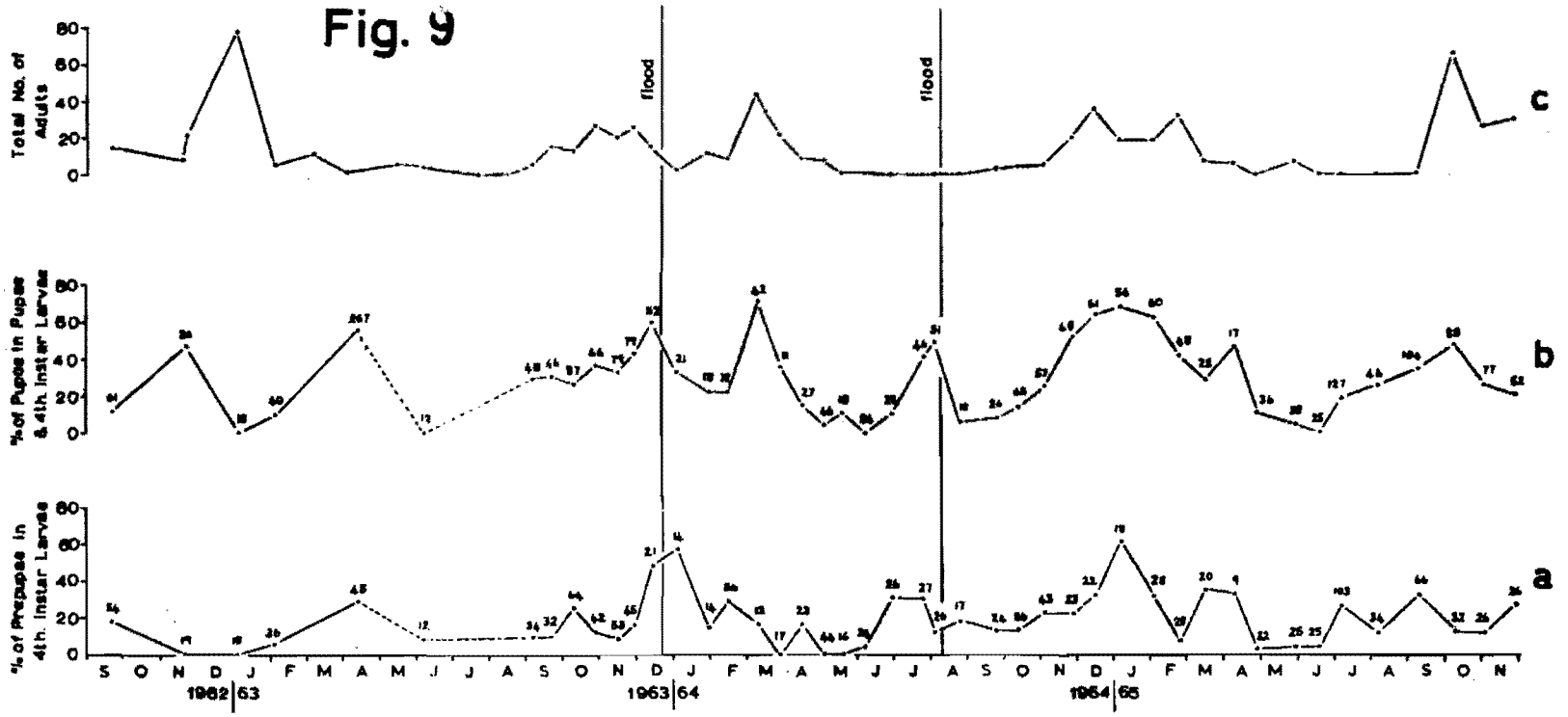
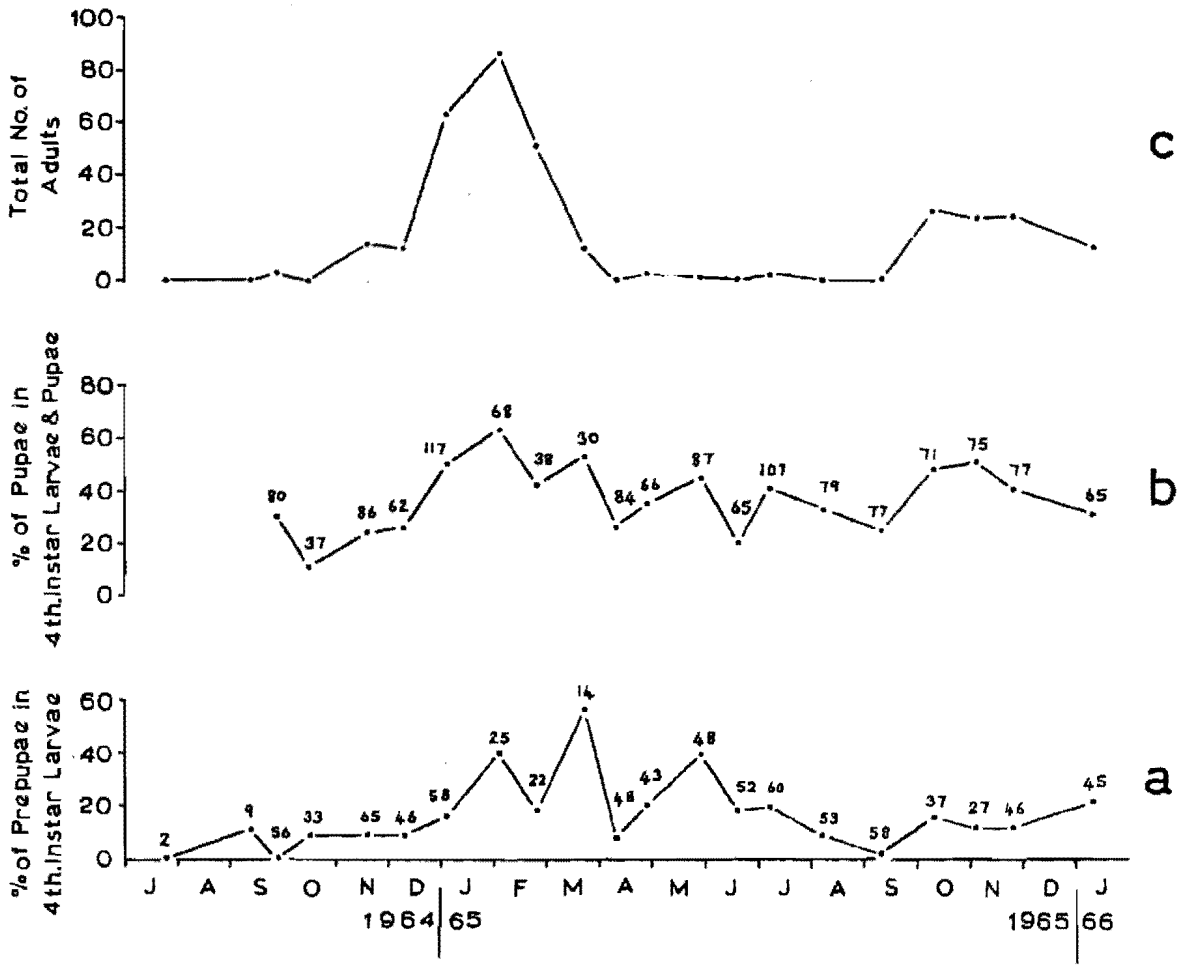

Total No. of Adults
% of Pupae in Pupae & 4th. Instar Larvae
% of Prepupae in 4th. Instar Larvae
flood
flood
c
b
a
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N
1962 | 63
1963 | 64
1964 | 65

Fig. 10


Total No. of Adults
100
80
60
40
20
0
c
% of Pupae in 4th.Instar Larvae & Pupae
80
60
40
20
0
80 37 86 92 117 138 68 130 84 96 87 65 101 79 77 71 75 77 65
b
%of Prepupae in 4th.Instar Larvae
60
40
20
0
2 9 56 33 65 46 58 25 22 14 48 43 48 52 60 53 58 37 27 46 45
a
J A S O N D J F M A M J J A S O N D J
1964 65
1965 66

Only adults of N. campbelli were measured to check any seasonal change in size, as N. hudsoni and P. turrifer have shorter emergence periods and fewer were collected.

Life Cycles.

Purau and Kaituna: At Purau and Kaituna adults of Neocurupira chiltoni were found almost all the year with the greatest number occurring between September and May (Fig. 9c and 10c). The number of pupae taken (as percentages of pupae in pupae+fourth instar larvae collections), however, shows two peaks per year, one during the spring and the other during autumn (Fig . 9b):-

	Autumn Peak.	Spring Peak.
1962	-	November.
1963	April.	November.
1964	March.	July-January.
1965	April.	October.

The peak pupal numbers during spring give rise to the main peak in adult numbers. There is not such a great increase in adult numbers following the autumn peak. The reasons for this are not clear, but it may be due to a higher mortality of the pupae as a result of falling temperatures and higher water levels, or less likely, to sampling errors.

The peak number of prepupae generally preceeds the peak numbers of pupae and adults (Fig. 9a and 10a).

The August 1964 flood had a marked effect on the winter-spring increase in pupae, producing a later peak of pupae during January 1965. Because of this, the peak number of adults was delayed until December. The December 1963 flood appeared to have little effect on the proportions of pupae or adults, probably as the main peak of pupae was almost past

Fig. 11

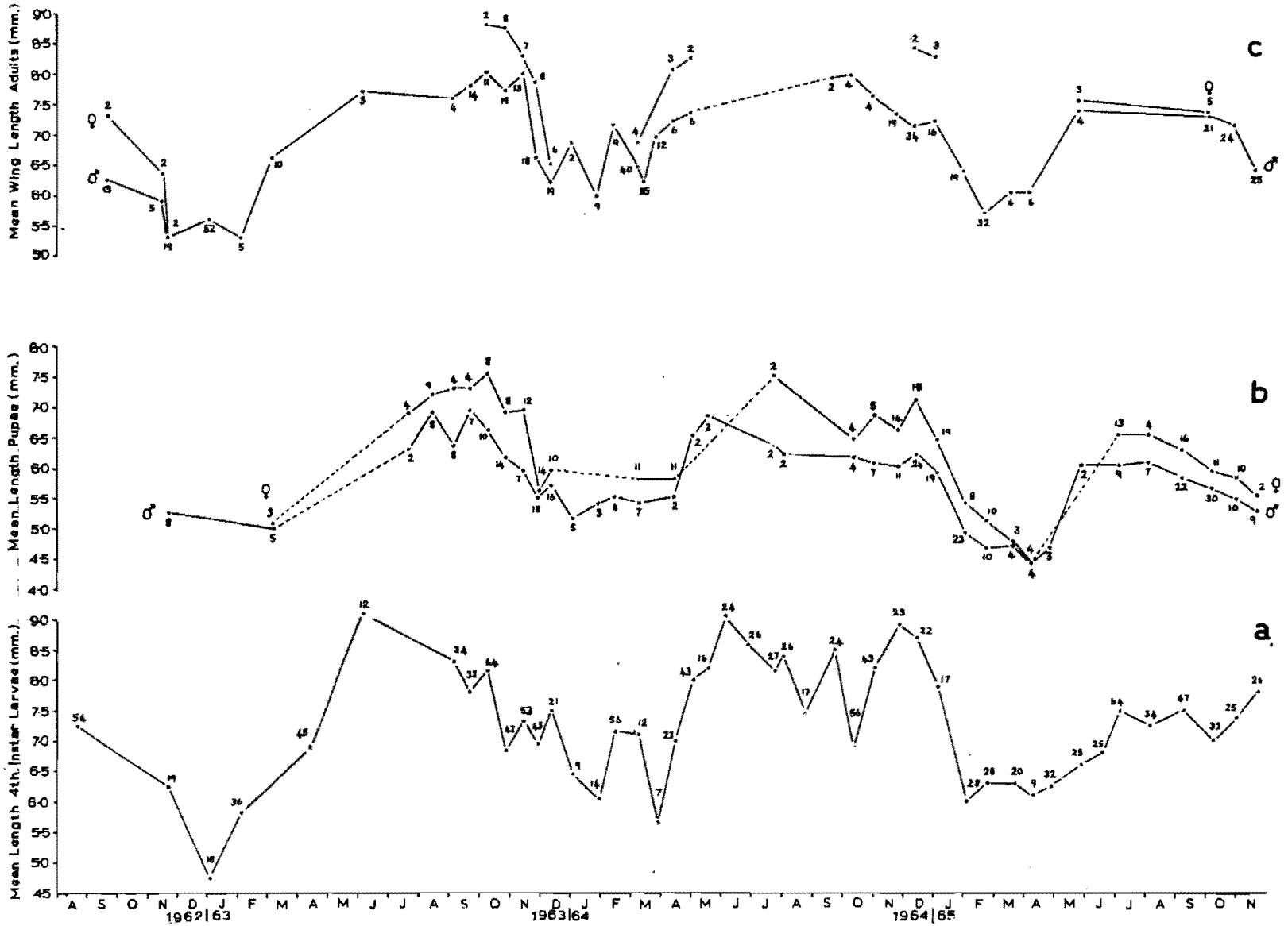
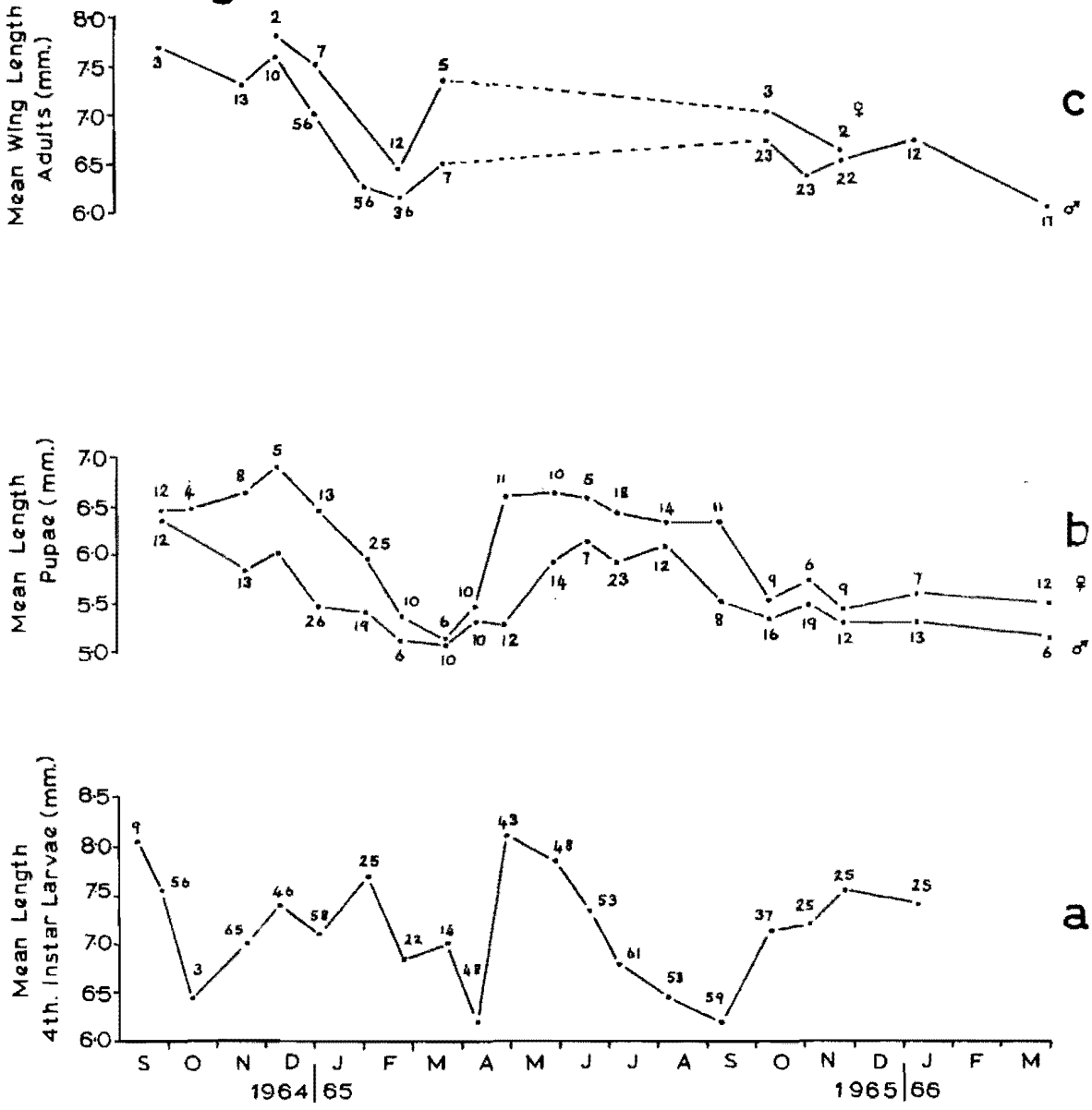

Mean Wing Length Adults (mm.)
Mean Length Pupae (mm.)
Mean Length 4th. Instar Larvae (mm.)
c
b
a
♀
♂
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N
1962|63
1963|64
1964|65

Fig. 12


Mean Wing Length Adults (mm.)
8·0
7·5
7·0
6·5
6·0
c
♀
♂
Mean Length Pupae (mm.)
7·0
6·5
6·0
5·5
5·0
b
♀
♂
Mean Length 4th. Instar Larvae (mm.)
8·5
8·0
7·5
7·0
6·5
6·0
a
S O N D J F M A M J J A S O N D J F M
1964|65
1965|66

at the time of the flood.

Kitakami (1950) states that blepharocerids with a summer-type life cycle (p.65) can complete the development of a generation within two months.

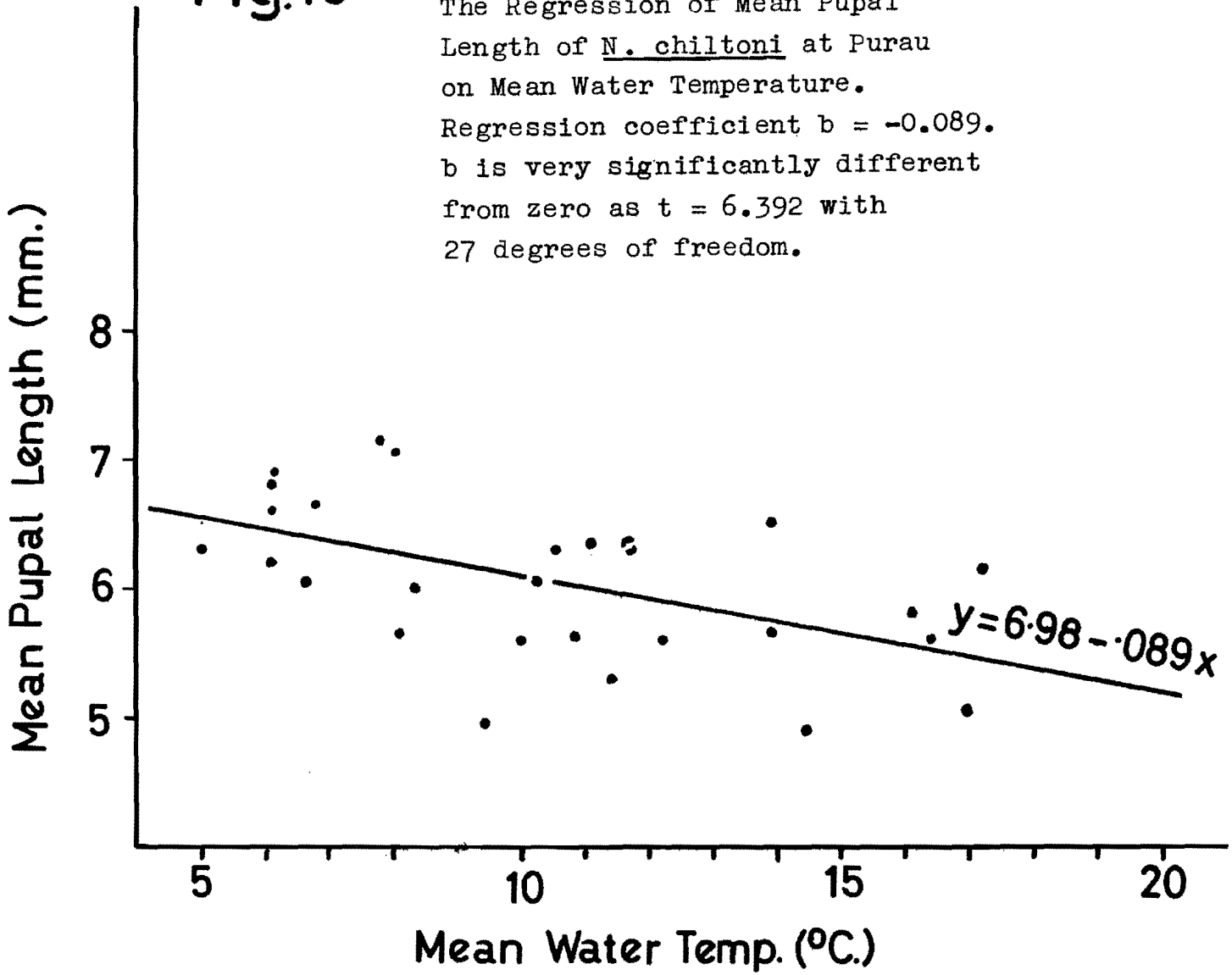
It is postulated here that the length of the emergence period of N. chiltoni and the warm temperatures experienced at Purau and Kaituna during the emergence period are sufficient for at least one other generation to complete development before winter.

Eggs laid during early September and October, would hatch within a month and a half (see Chpt. I for rates of development) and the resultant larvae would develop rapidly in the high temperatures, giving adults that would lay eggs, to form the adult population of the following summer. The rapid development could result in smaller larvae and subsequently smaller pupae and adults. Eggs laid in the latter part of the emergence period would be delayed in development by the lower temperatures as would the resulting larvae. The slower development could produce larger larvae and hence larger adults.

This hypothesis is supported by the observed seasonal change in the mean lengths of fourth instar larvae, pupae and adult wings (Figs. 11 and 12). The largest larvae, pupae and adults are found during spring at the beginning of the emergence period, presumably having developed slowly during the winter. As the season advanced the size of the larvae, pupae and adults decreases, reaching a minimum in late summer months (February, March, April). Then as the temperatures become cooler the size of the instars increases and reaches a maximum at the end of the emergence

Fig.13

The Regression of Mean Pupal Length of N. chiltoni at Purau on Mean Water Temperature.
Regression coefficient b = -0.089.
b is very significantly different from zero as t = 6.392 with 27 degrees of freedom.



period. The seasonal changes in the mean pupal lengths show a significant negative regression on mean water temperatures (Fig. 13).

This hypothesis is similar in principle to that of Glendhill (1959) who reported a seasonal variation in adult size of Ameletus inopinatus (Ephemeroptera), with a decrease in adult size during emergence period. He suggested that the larger imagines arose from nymphs that grew throughout the winter, and that the smaller imagines arose from eggs that hatched later and presumably developed more rapidly during the warmer period.

Stuckenberg (pers. comm. 1964) described a life cycle, similar to that of Neocurupira chiltoni, for Elporia flavopicta which appears to have at least two generations per year, one of which develops during winter and "hatches" during the spring with the "other (s)" completing their development during the late spring and summer months. He also noted that the winter larvae have the longest period of development and appeared larger than those developing during the warmer period.

Bealey Chasm: Of the Bealey Chasm blepharocerids (Neocurupira campbelli, N. hudsoni and Peritheates turrifer) the life cycle is best known for N. campbelli and most of the following description is based on this species.

The emergence period of the Bealey Chasm species is short compared with that of N. chiltoni at Purau (Figs. 9c, 14f, 15e and 16g).

There appears to be a single peak of egg hatching each year after the period of maximum adult numbers, which shows as an increase in the number of first instar larvae.

Fig. 14

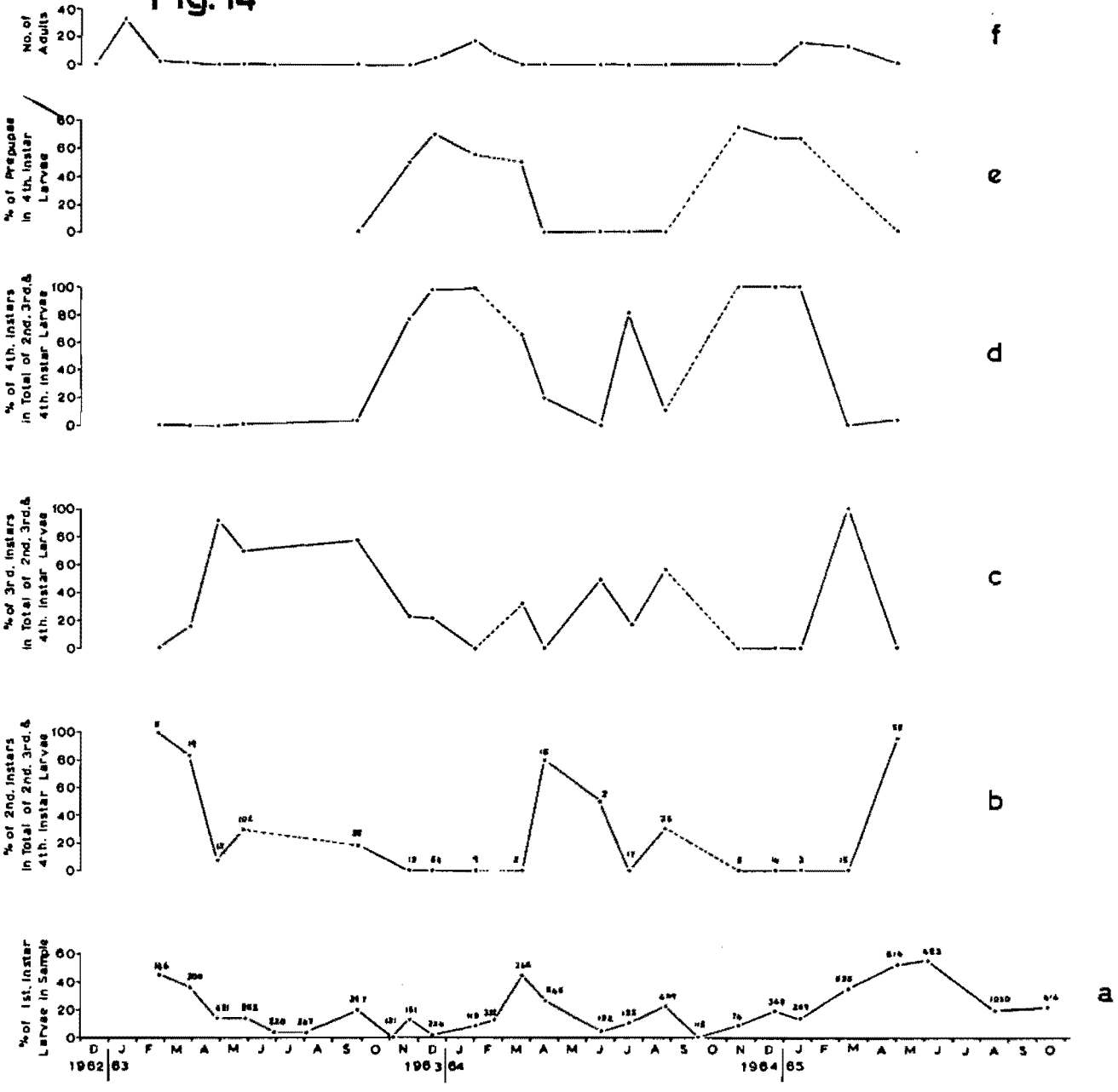

No. of Adults
f
% of Prepupae in 4th. Instar Larvae
e
% of 4th. Instars in Total of 2nd. 3rd. & 4th. Instar Larvae
d
% of 3rd. Instars in Total of 2nd. 3rd. & 4th. Instar Larvae
c
% of 2nd. Instars in Total of 2nd. 3rd. & 4th. Instar Larvae
b
% of 1st. Instar Larvae in Sample
a
D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O
1962 63
1963 64
1964 65

Fig. 15

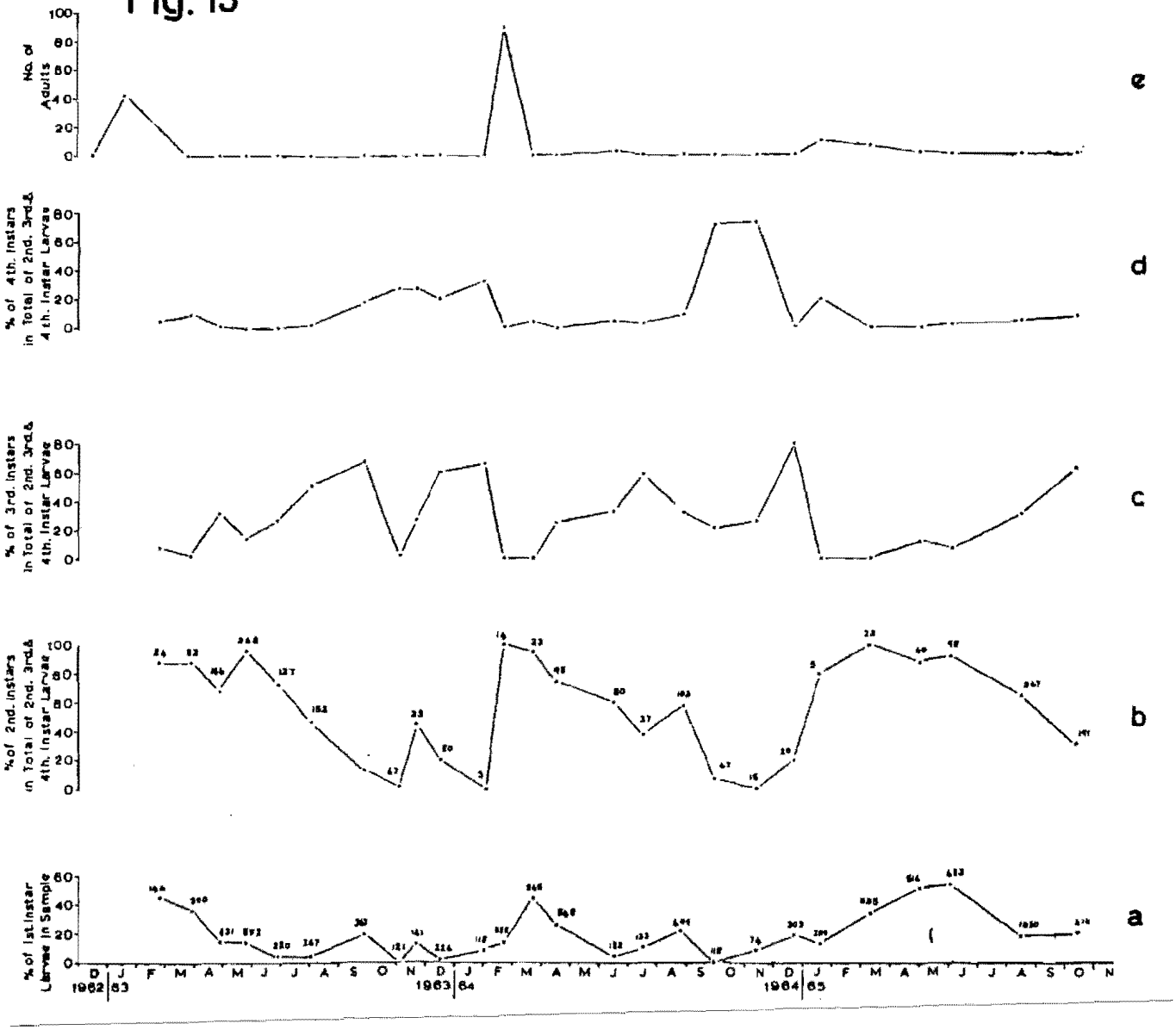
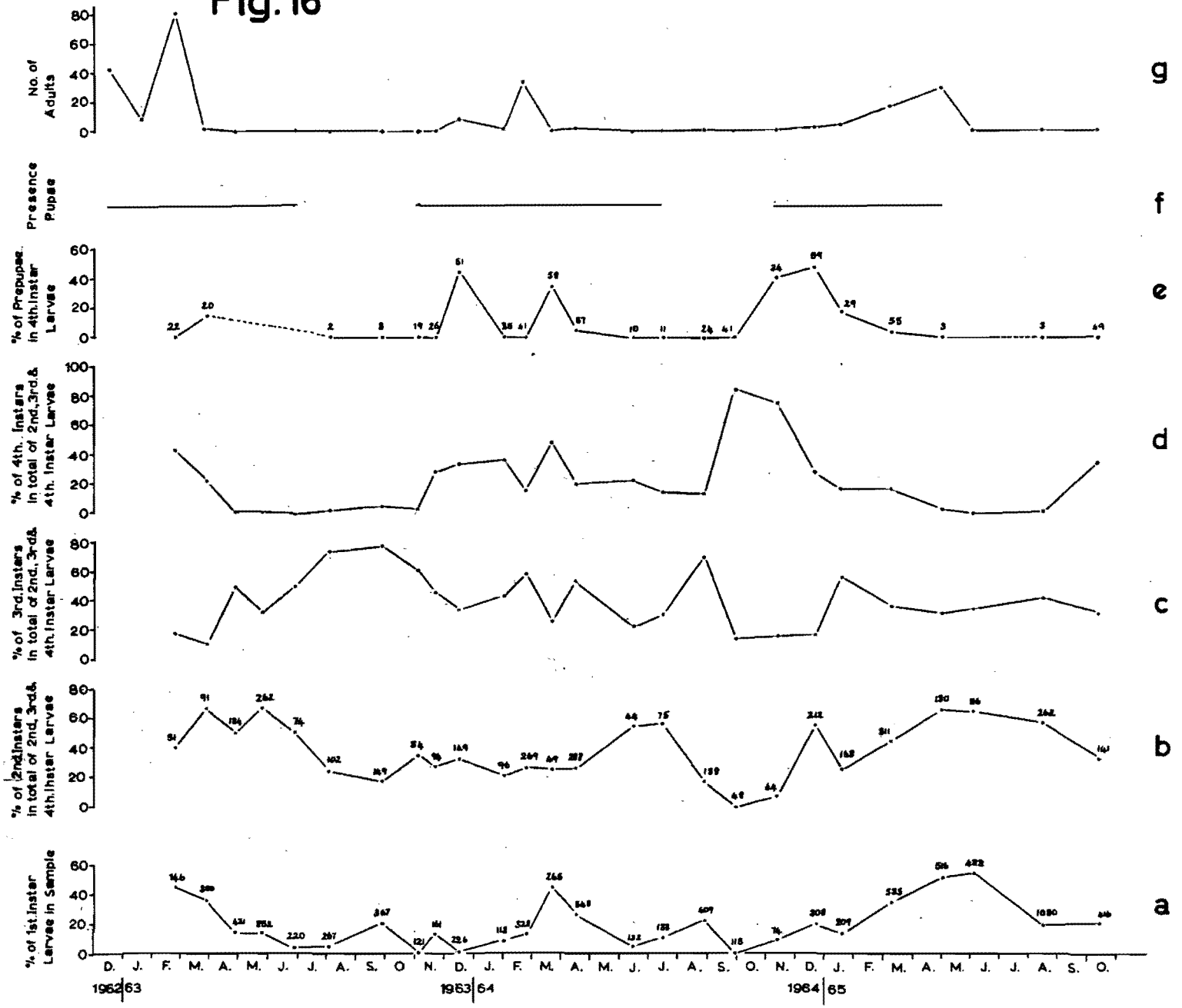

No. of Adults
e
% of 4th. Instars in Total of 2nd. 3rd.& 4th. Instar Larvae
d
% of 3rd. Instars in Total of 2nd. 3rd.& 4th. Instar Larvae
c
% of 2nd. Instars in Total of 2nd. 3rd.& 4th. Instar Larvae
b
% of 1st. Instar Larvae in Sample
a
D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N
1962 63
1963 64
1964 65

Fig. 16


No. of Adults
g
Presence Pupae
f
% of Prepupae in 4th. Instar Larvae
e
% of 4th. Instars in total of 2nd., 3rd. & 4th. Instar Larvae
d
% of 3rd. Instars in total of 2nd., 3rd. & 4th. Instar Larvae
c
% of 2nd. Instars in total of 2nd., 3rd. & 4th. Instar Larvae
b
% of 1st. Instar Larvae in Sample
a
D. J. F. M. A. M. J. J. A. S. O. N. D. J. F. M. A. M. J. J. A. S. O. N. D. J. F. M. A. M. J. J. A. S. O.
1962 63
1963 64
1964 65

(As it is not yet possible to identify first instar larvae to species level (Chpt. I), the percentages of first instar larvae in the samples taken, therefore, have been plotted on the figures for each of the species considered.)

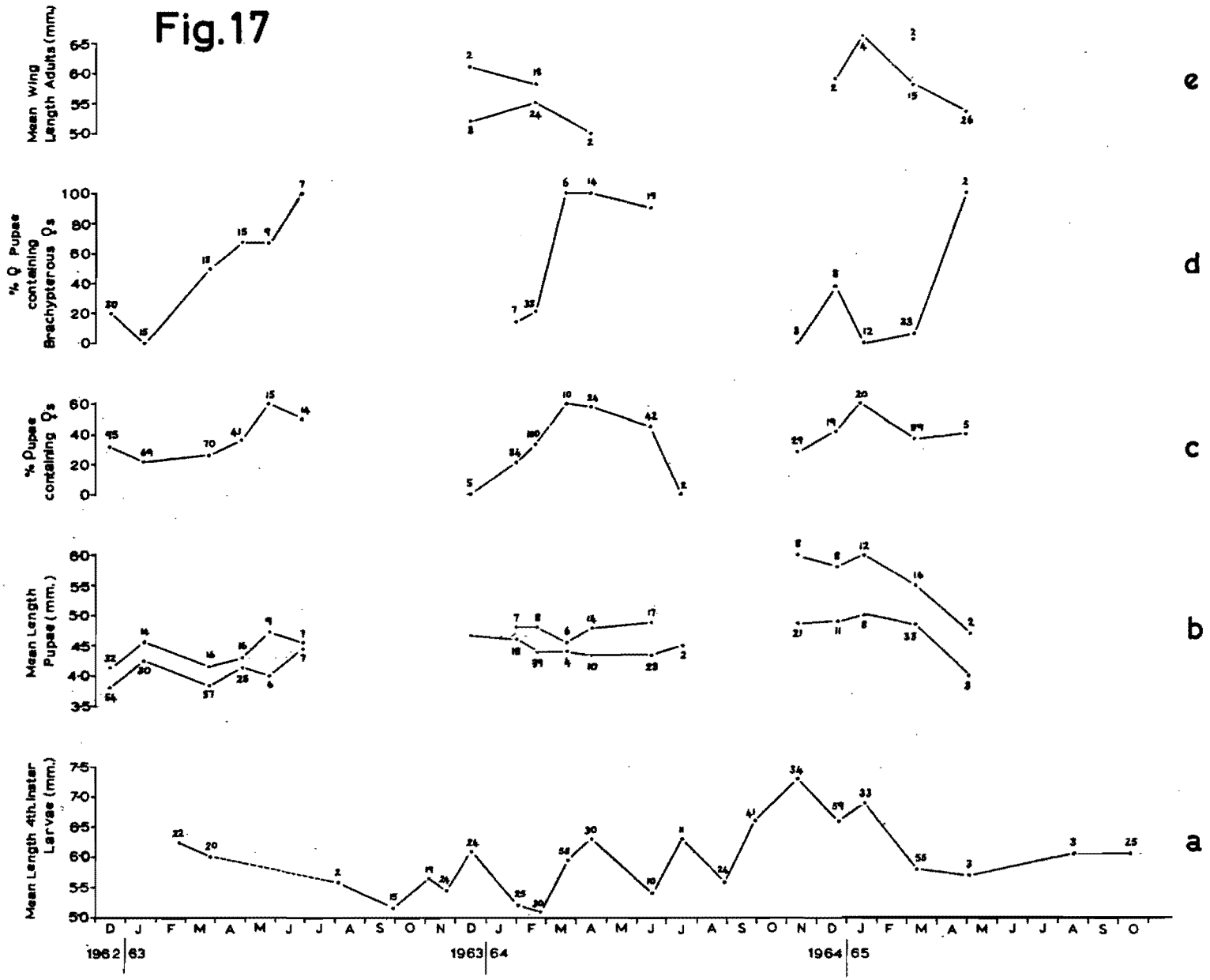
The progress of the first instar larvae can be followed through to adults emerging in the following year. This pattern of development shows particularly clearly for the 1964 peaks of the various instar stages of N. campbelli (Fig. 16). It does not show as clearly for N. hudsoni or P. turrifer, as smaller numbers of all stages were collected (Figs. 14 and 15). Both in N. campbelli and in N. hudsoni, during 1963 and 1964, though not in 1965, there were two subsidiary peaks as well as the main peak in first instar larvae numbers each year. These peaks probably represented the hatching of eggs laid late in the emergence period and delayed by the low temperatures of winter. The subsidiary peaks would then reflect an embryonic period of 6-10 months.

The fate of the larvae in the subsidiary peaks is not clear. In N. campbelli the first subsidiary peak (September 1963) can be traced through to prepupae of March 1964. These probably pupate for the numbers of prepupae decrease and collections of pupae have been taken up to July 1964.

It is not likely that many of these pupae survive the winter as most pupal aggregations at this stage are attacked by the fungus Aquamortierella elegans and Saprolegnia sp., or are removed by floods well before the new season's pupal aggregations form.

The mean lengths of fourth instar larvae, pupae and adult wings of N. campbelli (Fig. 17), in contrast to those

Fig.17


Mean Wing Length Adults (mm.)
% ♀ Pupae containing Brachypterous ♀s
% ♀pupae containing ♀s
Mean Length Pupae (mm.)
Mean Length 4th. Instar Larvae (mm.)
a
b
c
d
e
D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O
1962 63
1963 64
1964 65

of N. chiltoni do not show any significant seasonal changes.

Discussion.

Mannheims (1935) believed that the general life history of the blepharocerids of the Tyrol Mountains consisted of a single generation per year, even though the adults flew and laid eggs over an extended period and all stages of the life history were present at the same time.

Kitakami (1950) after an extensive study, grouped the Japanese blepharocerids into three groups, based on the life cycles:-

Winter-type. The eggs hatch in the autumn, larval growth takes place during winter, with pupation and emergence in the spring.

Summer-type. Different stages of development found during the summer, the "resting" stage occurring during winter.

Perennial-type. Larvae, pupae and adults found throughout the year.

Stuckenberg (1958) used Kitakami's categories for the life cycles of various species of Paulianina. The New Zealand blepharocerids studied here, however, do not fall readily into Kitakami's categories. The life cycles of the Bealey Chasm blepharocerids fall within Kitakami's winter-type cycle, but are irregular in that they have subsidiary peaks of larvae. N. chiltoni with more than one generation per year could be placed in the summer-type life cycle, but lacks the "resting" stage during the winter which is common

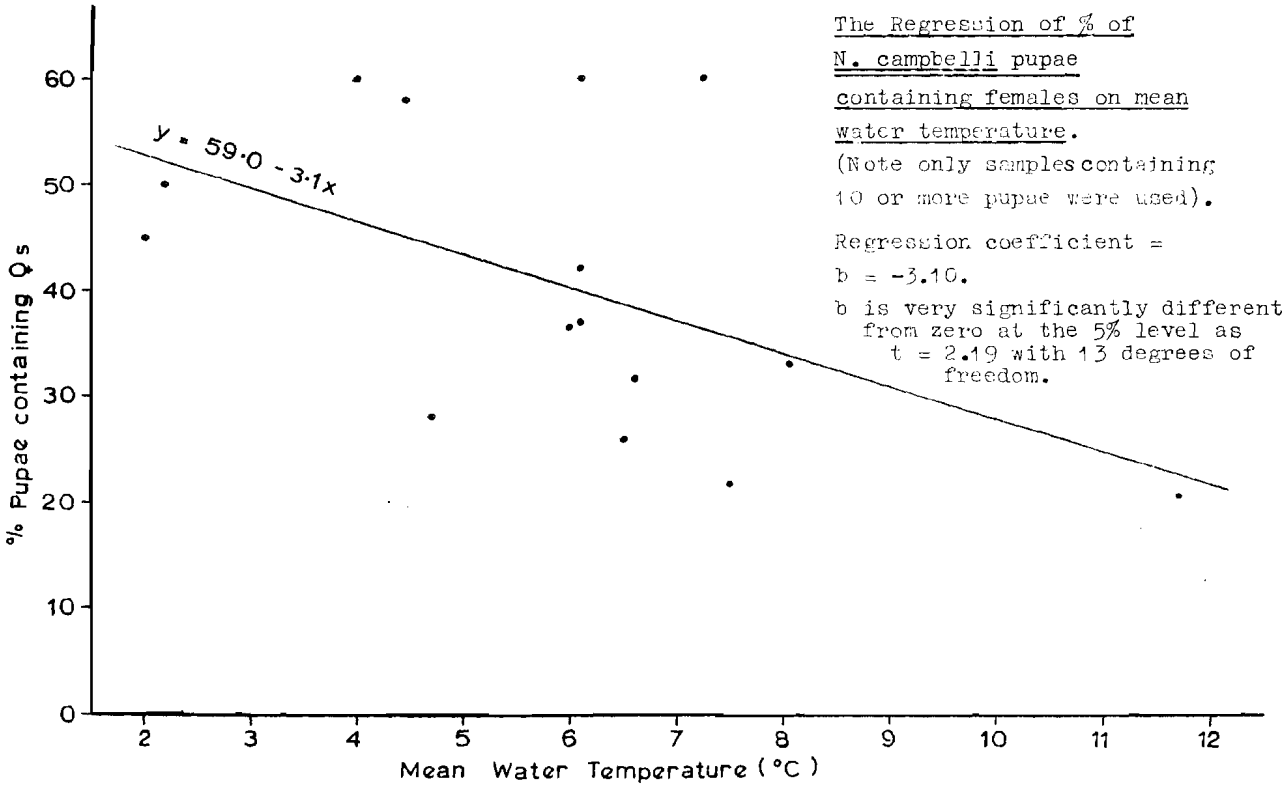
to species with this type of life cycle. On the other hand, with larvae present throughout the year N. chiltoni is more like the winter-type of blepharocerid.

It is suggested here that the life cycles of the blepharocerids occurring at Purau, Kaituna and Bealey Chasm are similar and correspond generally to Kitakami's winter-type life cycle. The differences in the cycles between Purau and Kaituna on the one hand, and Bealey Chasm on the other, are considered to result from the differences in temperatures between these localities.

At Bealey Chasm eggs laid up to mid-summer produce the next season's adults, while those laid late in the season do not hatch until mid-winter and give rise to the subsidiary peaks of larvae.

The longer summer at Purau and Kaituna allows eggs that have been laid early in the season to develop rapidly into adults, so that there is probably more than one generation produced each year.

Fig. 18



The Regression of % of *N. campbelli* pupae containing females on mean water temperature.
(Note only samples containing 10 or more pupae were used).

Regression coefficient =
b = -3.10.

b is very significantly different from zero at the 5% level as t = 2.19 with 13 degrees of freedom.

Sex Ratios.

Collections of blepharocerid adults, with the exception of Peritheates turrifer, from the study areas rarely contained as many females as males. Mannheims (1935) has also commented upon the fact that there are generally ~~less~~ fewer females than males.

Collections of P. turrifer on the other hand usually contained as many females as males.

The preponderance of males in the other collections is probably due mainly to the behavioural difference between the sexes, and possibly to differing life spans. However, the sex ratio at emergence exerts some influence.

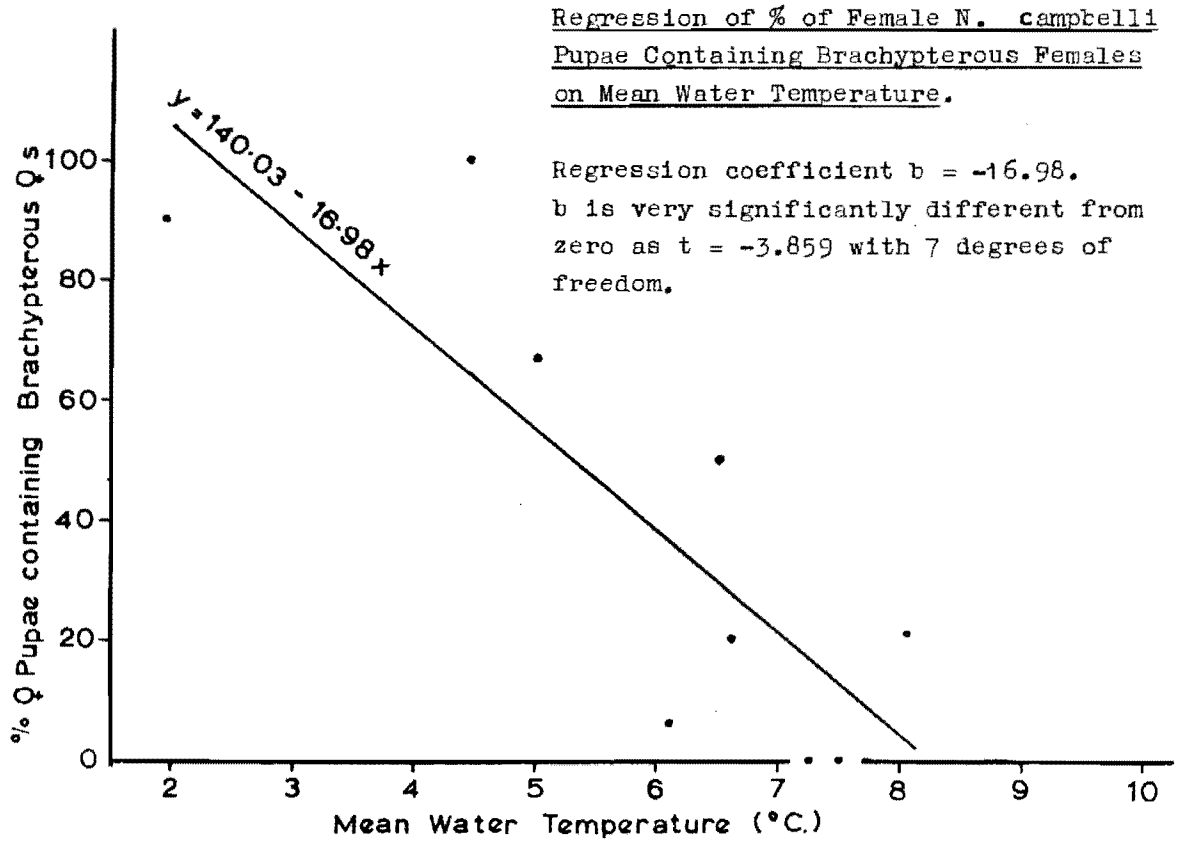
The sex ratio of pharate P. turrifer adults is not significantly different from a 1:1 sex ratio, whereas the sex ratios of both Neocurupira campbelli and N. chiltoni differ significantly ($p < .005$ in both cases) from a 1:1 sex ratio. This agrees in general with the sex ratios of the adults.

The sex ratio of pharate N. chiltoni adults from both Purau and Kaituna is relatively constant throughout the season, but that of N. campbelli shows a significant ($p < .005$) variation (Fig. 17), and shows a significant negative regression on mean water temperature (Fig. 18).

The determination of sex in some insects (particularly Drosophila) is known to be not purely dependent on the segregation of the "sex" chromosomes (Sinnott, Dunn and Dobzhansky 1958, and Gardiner 1964). Sinnott et. al. states that sex "is determined by the interaction of the genotype with the environment".

It is possible that the sexuality of N. campbelli is affected by temperature at some early stage in the life cycle.

Fig. 19



Regression of % of Female N. campbelli Pupae Containing Brachypterous Females on Mean Water Temperature.

Regression coefficient b = -16.98.
b is very significantly different from zero as t = -3.859 with 7 degrees of freedom.

Brachypterism.

Brachypterism in the Blepharoceridae was first recorded by Dumbleton (1963a) in pharate Neocurupira campbelli females. Brachypterous N. campbelli female adults have been collected during the present study, as well as a single example of a brachypterous pharate N. hudsoni male (Chpt. I).

Dumbleton stated that there was then no evidence to suggest any seasonal variation in brachyptery. But analysis of the more extensive collections of N. campbelli adults made during this present study shows a seasonal variation, in which brachypterous females are confined to the autumn (March-June).

Examination of the pupae collected from Bealey Chasm shows that there is a similar variation in the number of brachypterous pharate females (Fig. 17). The percentage of brachypterous pharate females present in the population at different times shows a highly significant negative regression on temperature (Fig. 19).

Considering the large numbers of pupae that contained brachypterous females, it is surprising that no more than six brachypterous females have been collected. This may indicate that the genotype of the brachypterous females is in some way deleterious and that the adults fail to emerge, or more probably that they are missed during collecting for they cannot fly (Chpt. I) and only crawl over the rocks near the pupal aggregations.

Lack of ability to fly does not preclude brachypterous females from mating. Two of the six specimens collected were taken while mating with normal males, and the other four were ovipositioning at the time of capture, presumably having already mated.

Causal effects of brachypterism have been considered by Brinkhurst (1959), Downes (1965), Young (1965) and others. Similar studies have yet to be made on the brachypterism in blepharocerids and little is known at the present time.

However, the fact that both the percentage of brachypterous female pupae and the percentage of female pupae of N. campbelli show significant negative regressions on mean water temperatures, strongly suggests that the variations in brachypterism and sex ratios are interrelated.

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CONCLUSION

Tillyard (1922) stated that "In all stages of their life-history, Blepharoceridae are dependent on the rushing water and spray of waterfalls, and are quite unable to exist for more than a very short time without these. Hence their distribution cannot have been brought about by sea or air carriage, but must have taken place along definite land routes marked by the frequent occurrence of running streams; and this of course, indicates land of a mountainous nature". With the possible exceptions of some examples of aerial distribution of the Blepharoceridae (Edwards 1929 and this work, Chapter I), Tillyard's statement is fully supported here.

All known New Zealand blepharocerid habitats possess, (1) a swift, continuous, flow of clear water, which is sufficient to keep portions of the bed free from vegetation, (2) a relatively stable bed, with some larger rocks to provide refuge from flood scouring for larvae and pupae, and (3) rocks which protrude above the water level for ovipositioning, (the tributary of Pu Pu Springs River, Takaka is exceptional as no rocks protrude above the water level).

New Zealand blepharocerids occur in almost all the suitable habitats examined, their absence from some apparently suitable situations close to known blepharocerid localities is at the moment unexplained. Similar discontinuities in blepharocerid distribution elsewhere have been commented upon by Kellogg (1903) and Alexander (1963).

The fauna associated with blepharocerid larvae in Bealey Chasm and in other similar habitats is impoverished compared with that in Purau Stream and in certain high altitude streams. This probably results from the high water velocity and lack of suitable habitats for associates at Bealey Chasm. Dactylocladius commensalis originally considered to be specific to N. hudsoni larvae has now been found associated with larvae of other members of the hudsoni-complex and occasionally with N. campbelli larvae. Known predators of New Zealand blepharocerids include Trichoptera, Neuroptra and

Plecoptera larvae and spiders, while parasites include fungi, nematodes and mites.

The preference of blepharocerid larvae for fast flowing water may be determined by their high respiration rate and their immovable tracheal gills which are situated on the ventral surface close to the suckers and are therefore close to the substrate. Neocurupira chiltoni larvae are much more tolerant of slower water than the other New Zealand species. The method of attachment to the substrate and the larval body shape are probably the main factors enabling blepharocerid larvae to inhabit situations where the water velocity is high. Some of the larval instars of the blepharocerids studied here appear to have different environmental preferences. First instar larvae remain around the empty egg cases, thus their distribution is determined primarily by oviposition behaviour. The second and third instar larvae, however, tend to be concentrated near the surface of the water, and the fourth instar larvae occur in deeper water and are more evenly distributed.

Blepharocerid larvae are unable to live in heavy growths of algae, even though they browse off the algal film covering the substrate. The maxillae are highly modified for scraping algae from the substrate.

Although adults have a well developed alimentary canal, there is no evidence to suggest that they do in fact feed. None have mouth parts adapted for predaceous feeding. Field observations indicate that the pharyngeal pump is used to take up water from the hygropetric zone of stones.

The presence of fully formed eggs in pharate females indicates that food is not necessary for egg maturation.

The oviposition behaviour of N. campbelli, N. hudsoni and P. turrifer (in which eggs are placed in the hygropetric zone) is similar to that reported for other blepharocerids (Mannheims 1935, Alexander 1963 and Giudicelli 1964). However, N. chiltoni and probably N. tonnoiri oviposite under the water level.

The differing life cycles of the blepharocerids studied are considered to be the result of the temperature differences experienced in the habitats rather than species differences in basic life cycle type.

The rate of embryonic development of N. chiltoni is relatively constant below approximately 10°C but increases rapidly above this temperature.

The summer period at Purau and Kaituna appears to be sufficiently long and warm to enable eggs laid early during the long emergence period to complete development and for the resulting adults to produce another generation before winter. The larvae, pupae and adults that develop quickly during the summer are smaller than those that develop more slowly during the winter. The summer period at Bealey Chasm is shorter and cooler than that at Purau, and eggs laid at the beginning of the short emergence period give larvae that develop during the winter to form the adult population of next summer. Eggs laid later in the emergence period at Bealey Chasm are delayed by the low temperatures and do not hatch until mid-winter. They complete their development during the following summer and pupate during the autumn, thus taking approximately 18 months to reach this stage. Collections of pupae and adults indicate that very few adults emerge from these pupae as the majority are later attacked by fungi or are destroyed by the winter and the spring floods, so that in general there is only a single generation per year of the blepharocerids at Bealey Chasm.

The increase in the numbers of pharate females and in the numbers of pharate brachypterous females of N. campbelli, towards the close of summer, appears to be related to a fall in temperature. In N. chiltoni, however, the sex ratio of pharate adults remains relatively constant throughout the year, despite the seasonal changes in temperature.

The embryonic development of N. chiltoni shows that the cephalic division consists of the head, thorax and first abdominal segment, that the median divisions each consist of a single abdominal segment,

and that the anal division consists of four fused abdominal segments. The development of the abdominal prolegs suggests that they are homologous to the thoracic prolegs. It is concluded that the embryonic development of the blepharocerids studied indicates phylogenetic affinities to the simuliids.

It is considered here that the Apistomyiinae originated in Asia from an ancestor that possessed holoptic-eyed males, forked Rs vein and long labial palpi. It is further believed that this ancestor invaded New Zealand along land connections during the late Cretaceous. There is no evidence that the Australian blepharocerids gave rise to the New Zealand forms. The orogeny, marine transgressions and the glaciation of New Zealand may all have contributed to the evolution of the present taxonomic situation within the blepharocerids.

The intrageneric variation of eye structure in the New Zealand Neocurupira, is sufficient to make the subgenus Paracurupira, which was erected to include dichoptic eyed males, unwarranted.

The virtual New Zealand-wide distribution of blepharocerids, the wide range of forms within the hudsoni-complex, which suggest recent speciation, and the very large populations of blepharocerids in some habitats, suggests that, contrary to Osten-Sacken (1895) and Kellogg (1903), the Blepharoceridae, at least in New Zealand, are neither "decadent" nor a dying Family.

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THE OCCURRENCE OF NEMATODES IN THE FAMILY BLEPHAROCERIDAE (DIPTERA)

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Nematodes are known to occur as parasites of many groups of insects, but apart from a specimen collected by L.J.Dumbleton, have not been reported from New Zealand Blepharoceridae.

Pupae and adults of Blepharoceridae collected at Arthur's Pass, Canterbury, during the period December 1962 to June 1963, have been found to contain nematodes of the family Mermithidae. These have been further identified by Dr. W.C.Clark, as belonging in the genus Agamomermis. As yet nematodes have not been found in the larvae.

Mermithids were found in two of the three species of Blepharoceridae collected at Arthur's Pass. Although many pupae and adults were examined, only 35 Neocurupira campbelli Dumbleton, and 2 Peritheates turrifer Lamb contained nematodes, while Neocurupira hudsoni Lamb showed no signs of parasitism.

The number and size of the nematodes varies, but no more than three have been found in any one host. There is a tendency for nematodes that occur singly to be larger, 19-30 mm. in length, while those that occur in numbers of two or three are smaller, 15-23 mm. The diameter of all the nematodes is

.15-.25 mm. Both N. campbelli and P. turrifer pupae are 4-5 mm. long and 2.0-2.5 mm wide.

The effect of the nematodes on their hosts is variable. Some parasitised pupae contained well developed adults, while others showed a complete displacement of pupal tissues. All parasitised adults were active, but while males and some females showed no apparent effect, other females contained little else besides the nematodes.

APPENDIX 2.

(Reprinted from Tuatara Volume 14(2) July 1966)

TECHNIQUES FOR REARING STREAM-DWELLING ORGANISMS IN THE LABORATORY

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INTRODUCTION

Because of the relative ease with which pond organisms can be reared under laboratory conditions, the rearing of stream-dwelling organisms tends to be neglected. This article provides brief descriptions and a literature list of techniques used to rear stream organisms in the laboratory.

One difficulty in setting up an artificial stream is the transfer of stream fauna from their natural habitat to the laboratory. The death of fauna during transfer is caused usually by an inadequate oxygen supply and/or rapid increases in temperature.

The oxygen supply can be maintained at an adequate level if a small volume of water with a large surface area is continually agitated. Rapid agitation, however, may cause damage to delicate insect larvae. If large volumes of water are necessary for transport of fauna, an adequate supply of oxygen can be maintained by using an air bubbler. It is possible to construct a simple air bubbler from a large plastic funnel, by attaching a bubbler tube to the neck and directing the open end of the funnel into the windstream created by the vehicular transport (Fig. A.). This method of aeration, however, rapidly raises the water to air temperature.

TEMPERATURE CONTROL

Temperature may be controlled by using large mouthed "Thermos" flasks during transport. Large volumes of material can be transported with good temperature control by using expanded polystyrene "Chillybins".

FOOD

Growths of algae for browsing insect larvae can be obtained by seeding the artificial stream with natural stream water. However,

some species of Ephemeroptera larvae eat considerable amounts of algae and can easily eat all available food if large numbers of larvae are placed in the stream. In artificial streams where filtered tap water is used, food must be added for filter feeders. Yeast suspension has been used successfully by D.M.Woods (pers. comm.) to feed Simuliidae larvae.

TOXIC SUBSTANCES

Some town water supplies are highly toxic to many stream animals because of such additions and impurities as hypochlorite and heavy metal ions. Copper retaining screens were found to be highly toxic to Simuliidae larvae by Hartley (1955), who also mentions that other workers have experienced difficulties with contamination when the water supply was in contact with copper. D.M.Woods (pers.comm.) uses activated charcoal filters successfully to remove both hypochlorite and heavy metal ions. Because of possible contamination no metal should be in contact with the water contained in artificial streams.

TECHNIQUES

Techniques for rearing stream organisms in the laboratory vary considerably in the way the currents are produced, but can be placed into two broad categories:- (1) Open Systems and (2) Closed Systems.

1. Open Systems: These are the simplest types of artificial streams, but depend on the abundance and purity of local water supply. The simplest type of Open System stream splashes tap water over rocks and stones which have been brought to the laboratory with the organisms still attached. B.Mannheims (pers.comm.) has used this arrangement to rear Blepharoceridae larvae to adults. A similar arrangement uses a stream of water directed into jars of Petri dishes and allows the water to overflow to waste (Fig. B). Hartley (1955) and Carlsson (1962) used jars and Petri dishes respectively to rear Simuliidae larvae. Hartley says that if the vessels are not raised off the bench the larvae will eventually migrate down onto the bench. Tonnoir (1923) produced a cascade of water by arranging porcelain evaporating dishes on an inclined plane, so that the water poured from one to the other. This arrangement was used to rear Blepharoceridae larvae (Fig. C). To prevent larvae from escaping, gauze was attached over the pouring lip of the dishes. This arrangement is ideal for keeping species separated and lends itself to considerable modification. A trough with a stair-like base has been used by Thomas (1946) and by Dalmat (1955) to rear Simuliidae larvae.

Water flowing rapidly down plastic troughs has been used by D.M.-Woods to rear Simuliidae larvae, similarily concrete channels with glass observation ports have been used by Dorier and Vaillant (1954) to study the effect of current on numerous aquatic inver-

tebrates. Large (approximately 1" internal bore) plastic tubing with the water flowing through has been used by Carlsson to rear Simuliidae, and by the writer to rear Chironomidae, Blepharoceridae and Simuliidae.

A glass aquarium with a jet of water directed against one side below the water line provides a good basis for a general stream aquarium (Fig. D). The depth of water, current and substrate can be varied with ease. Both Tonnoir and Carlsson used similar methods to rear Blepharoceridae and Simuliidae and the writer has reared Chironomidae, Blepharoceridae, Ephemeroptera and Trichoptera using this arrangement.

2. Closed Systems: These types of artificial streams allow greater control of temperature, mineral nutrients, food and hydrogen ion concentration than Open System streams. Unfortunately, nearly all of the numerous methods of producing currents in these streams are completely dependent on electrical power.

By using a stirrer to produce a circular current in a jar (Fig. E), Philipson (1953) was able to study the feeding habits of Trichoptera larvae. However, to investigate the effects of water flow and oxygen concentration on 6 species of Trichoptera larvae, Philipson (1954) used jars with rotating glass stoppers which were lubricated with paraffin oil, the stirrers being attached to the inside centre of the stoppers. Whitford & Schumacher (1961) used a modified magnetic stirrer to study the effect of current on algal metabolism. In a similar method immobile plates were suspended

within a rotating jar of water (Fig. F). By oscillating jars in an horizontal plane a gentle circular current can be created. Freeden (1959) used these last two methods to rear certain species of Simuliidae larvae.

Air bubbled through water will produce sufficient turbulence or current to keep most stream organisms alive. However, Freeden reports that apparently the upper velocity limit of the water current produced by this method is 1.4 ft. per. second, this being inadequate for certain species of organisms. This method also rapidly raises the water to air temperature. Air bubbled up through an open tube (Fig. G) or up an inclined glass plane (Fig. H) suspended within a large volume of water forms the basis of the methods used by Puri (1925), Smart (1934), Makerras & Makerras (1948)and Davies and Smith (1958) for rearing Similiidae larvae. Doby, David & Rault (1959) have reviewed these and other methods for rearing Simuliidae. Simuliidae larvae have been reared in 10 ml. test tubes with air diffusers by Woods (Fig. I). This is a useful method when the volume of compressed air is limited.

Recirculating apparatus usually consists of a pump, a straight trough and a reservoir. The water is pumped from the reservoir either directly into the trough or firstly into an upper head-tank, and thence into the trough. Troughs in artificial streams of this type have been constructed from wood, earthenware, asbestos-fibre and perspex; self-priming certrifugal pumps appear to have been used rather than other types of pumps. Refrigeration units for temperature

control are usually placed in the reservoir. Using apparatus of this type, Zahar (1951), Wright (1957) and Hall & Harrard (1963) have reared Simuliidae; Moore (1964), freshwater snails; Whitford, Dillard & Schumacher (1964), lotic organisms, and Lauff & Cummins (1964), have studied lotic ecology.

Apparatus based on the recirculation principle has been used to study the metabolism of running water organisms. In these cases the stream was completely enclosed and airtight. Odum and Hoskins (1957) have studied algal metabolism, Gaufin & Gaufin (1961) the effect of oxygen concentration on Trichoptera larvae, and Brett (1965) the metabolism of Canadian salmon. Sudia (1951) used an oval galvanised iron tank to study the effects of water flow on mosquito larvae. The current was produced by nozzles directing the water around the trough.

The writer has constructed an artificial stream of the circulation type incorporating many of the ideas from other workers (Fig.J). The stream has been designed to provide a flexible piece of apparatus for use in as many fields of research as possible.

A fibre-glass centrifugal pump capable of delivering 700 gallons of water an hour, though not running to full capacity, is powered by a 1/3 h.p. intermittent-running electric motor. The water is pumped into a head-tank and is maintained at a set level by an off/on float switch which controls the motor and pump. A ball-cock valve which is connected to the tap-water supply becomes activated if the water in the head-tank falls below a minimum level. This

ensures a water flow in case of power failures or breakdown of the pump or motor. From the head tank the water flows down large-bore plastic tubes into the stream portion of the apparatus, a straight perspex trough, 3ft. x 6in. x 6in. Wells at each end of the trough help to break the flow of incoming water and facilitate the removal or addition of organisms and substrate. A nylon gauze barrier at the outlet of the trough retains the organisms. Small ridges on the base of the trough retain the substrate, which in this case consists of small stones. The trough is roofed with perspex plates. Above the trough is suspended a daylight-type fluorescent tube and a time switch to provide approximately daylight conditions. The light from the fluorescent tube is sufficient to allow growth of algae and Hepaticae. From the trough the water flows through a filter of activated charcoal and then into the reservoir. Heating and refrigerating units for temperature control are suspended in the reservoir. The total volume of water held in the complete apparatus is approximately 60 gallons.

This stream has performed without major trouble for approximately twelve months. Stream organisms reared successfully so far are, algae, Hepaticae, Turbellaria, Gastropoda, Ephemeroptera, Plecoptera, Neuroptera, Trichoptera, Chironomidae, Blepharoceridae and Simuliidae. The stream has also been used to study the effects of current on various species of N.Z.Galaxidae fish.

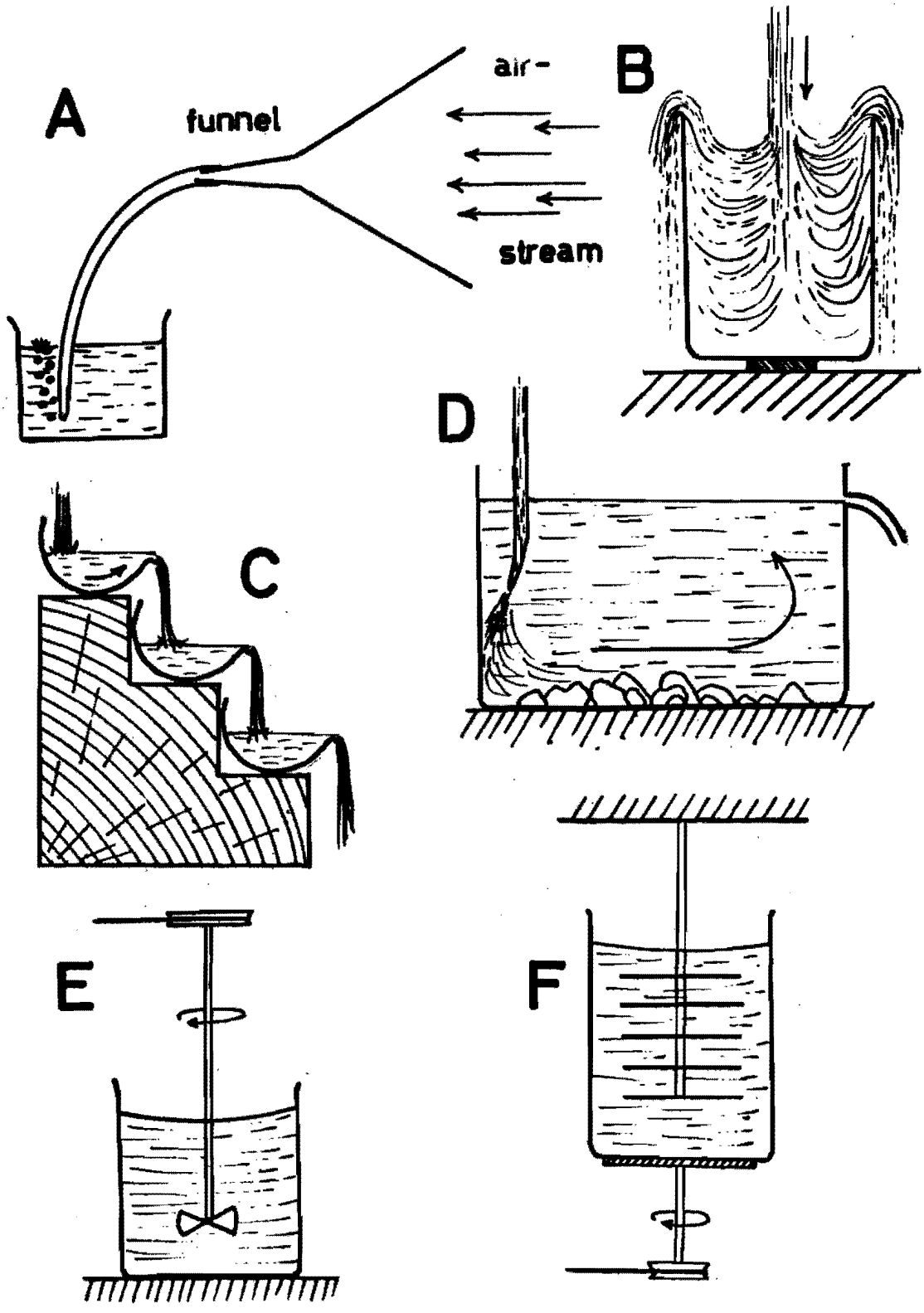
Figure A. A simple portable bubbler.

Figures B, C & D. Open system streams.

Figures E. & F. Closed System streams using rotating current.

Figures G, H & I. Closed System streams using compressed air.

Figure J. Closed System stream using recirculation.


A
funnel
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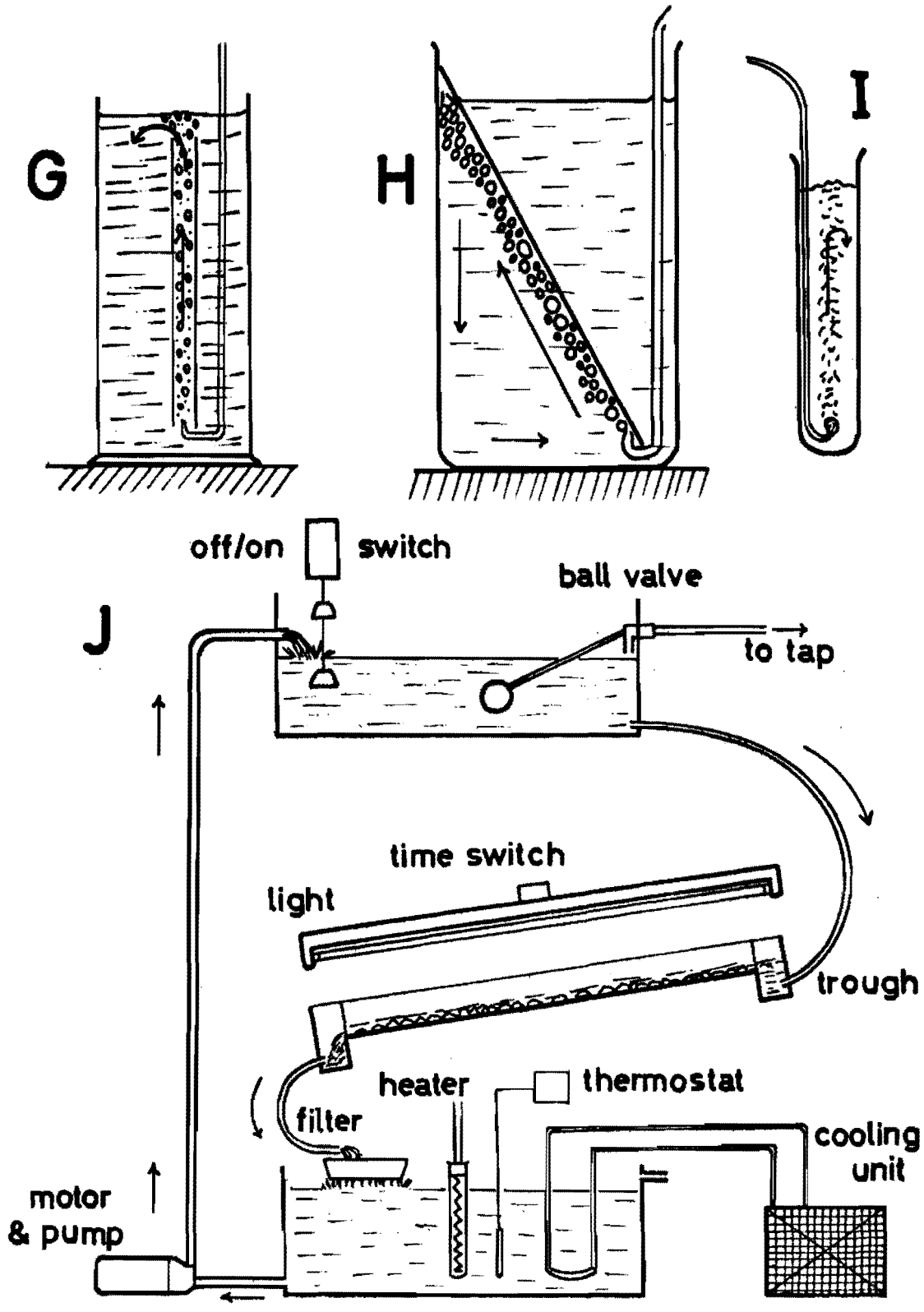
G
H
I
J
off/on switch
ball valve
to tap
time switch
light
trough
heater
thermostat
filter
cooling unit
motor & pump

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APPENDIX 3.

(Accepted for publication by the Transactions of the Royal Society of New Zealand.)

A REINTERPRETATION OF THE LARVAL MAXILLA OF THE BLEPHAROCERIDAE (DIPTERA, NEMATOCERA).

by

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ABSTRACT

The larval maxilla of Blepharoceridae is reinterpreted on evidence from the embryology of Neocurupira chiltoni and the maxillary musculature of larval N.chiltoni, N.hudsoni and Hapalothrix lugubris.

In the current interpretation of the larval maxilla of the Blepharoceridae (Müller, 1879 and Bischoff, 1928) as exemplified by Hapalothrix lugubris Leow (Fig. 1), the anterior lobe is termed the "Maxillarlade" (= lacinia), the median sensory lobe the "Maxillartaster" (= maxillary palp) and the posterior hook-covered lobe the "Mentallappen (Polster)" or "Almofadas" (="little cushion").

During the embryonic development of Anurida maritima (Collembola: Imms, 1906); Baetis vagans (Ephemeroptera:Needham, 1935); Lepisma saccharina (Thysanura:Johannsen and Butt, 1941); and Neophylax connicinnus (Trichoptera:Patten, 1884) and Calandra oryzae (Coleoptera: Teigs and Murray, 1938), the maxillary segments develop basal and distal lobe-like portions. The distal portion

grows posteriorly but then rotates to become anteriorly orientated and forms the maxillary palp.

The embryonic maxillary segments of Neocurupira chiltoni also develop basal and distal lobe-like portions and by the sixteenth day the distal portion (Fig. 2 Mxp) covers the lateral margin of the labial segment and a small portion of the prothoracic segment, but in this case does not rotate to form a typical maxillary palp. Rather the distal portion forms the "Mentallappen (Polster)" and the basal portion grows forward to form the "Maxillarlade" and "Maxillartaster".

Even though the distal lobe of the maxilla of N.chiltoni does not rotate and does not form a typical maxillary palp, the initial embryonic development of the maxilla follows so closely that of the other orders of insects, it is postulated that the "Mentallappen (Polster)" and not the "Maxillartaster" is the true maxillary palp.

This hypothesis is supported by the musculature of the larval maxilla. According to Das (1937) and Hinton (1958), dipterous larvae never have muscular insertions on the maxillary palp. Das further states that, though certain muscles may be lost in the larval maxilla, the cranial flexor muscle of the lacinia is always retained. Examination of the musculature of the maxilla of larval Neocurupira chiltoni, N.hudsoni Lamb and Hapalothrix lugubris Leow, shows that the sensory lobe previously interpreted as the maxillary palp is the only maxillary structure to have a

muscular insertion. Therefore it is concluded from the criteria of Das and Hinton, that the sensory lobe is the lacinia and not the maxillary palp. The remaining part of the maxilla, the anterior brush-like region previously interpreted as the "Maxillar-lade" or lacinia is probably the galae. However, a study of the complex maxillary sclerit es might clarify this point.

Figure 3 presents the new interpretation of the larval maxilla of the Blepharoceridae.

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Fig. 1. Ventral view of left maxilla of Hapalothrix lugubris. Interpretation after Bischoff and Müller.

L - Maxillarlarlade (= Lacinia).

Mxt - Maxillartaster (= Maxillary palp).

M(P) - Mentallappen (Polster).)
) (= "Little cushion").
Alm - Almofadas)

Fig. 2. Lateral view of sixteen day embryo of Neocurupira chiltoni.

Mn - Mandible.

Mx - Maxilla.

Mxp - Maxillary palp.

Lb - Labium.

Fig. 3. Lateral view of left maxilla of Neocurupira chiltoni.

G - Galea.

L - Lacinia.

Mxp - Maxillary palp.

Mus - Muscle.

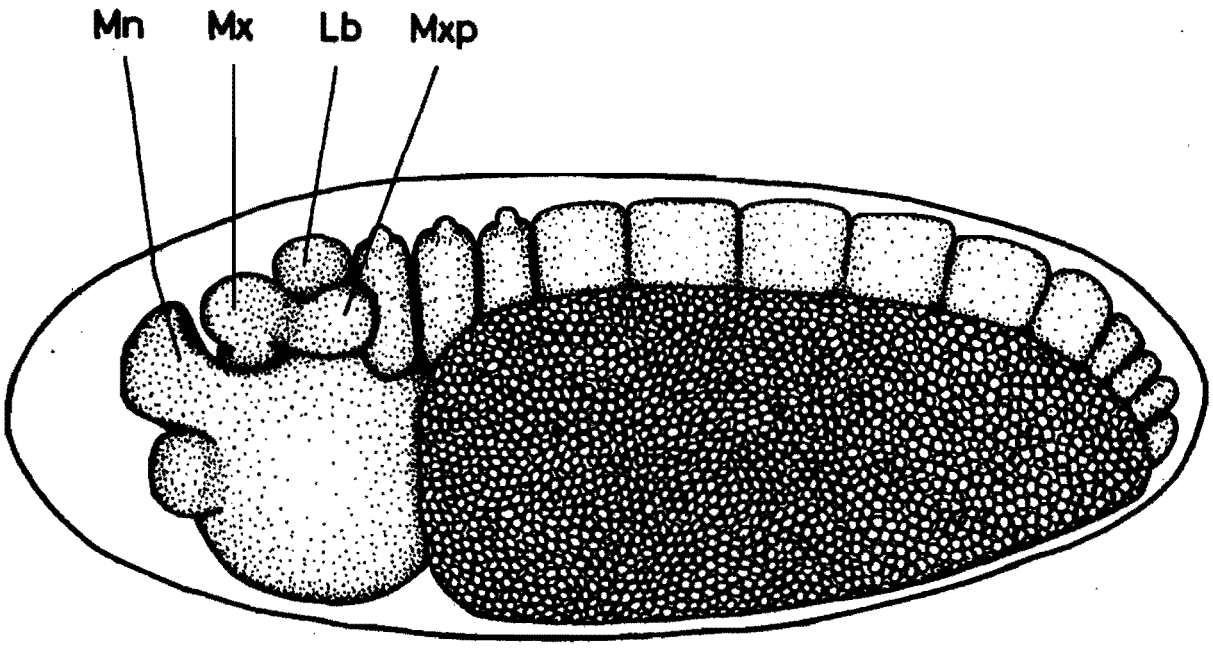


Fig 2

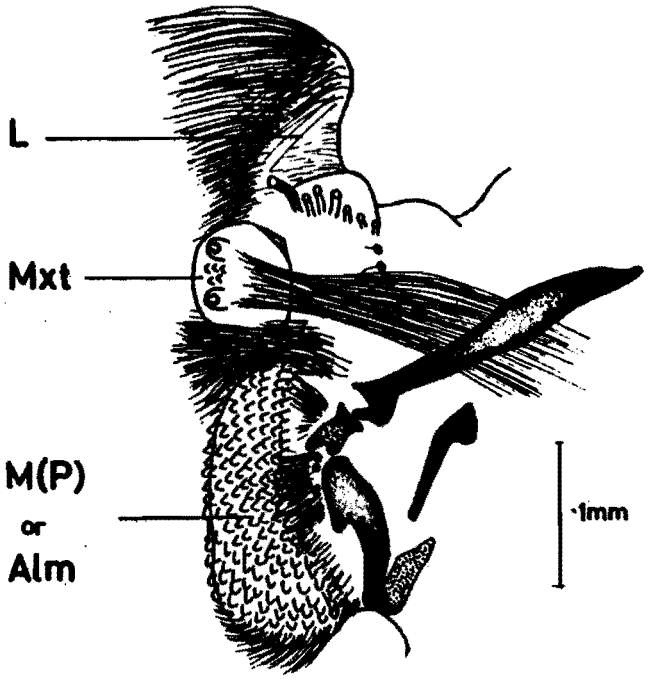


Fig 1

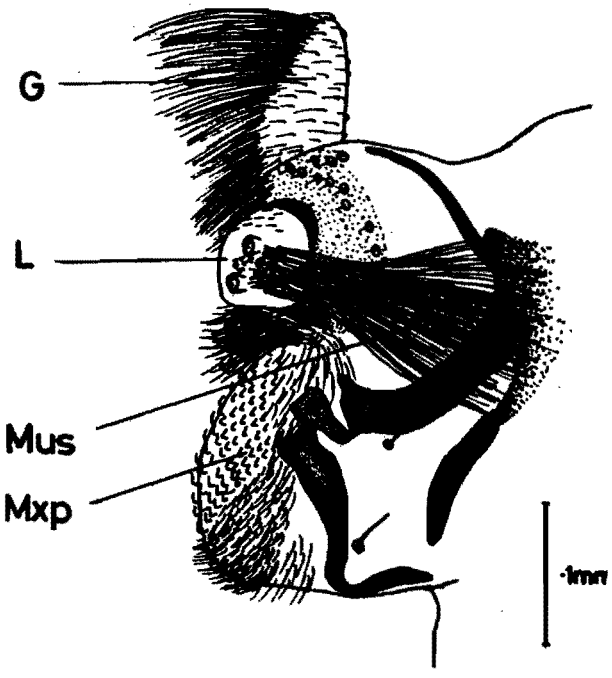


Fig 3

Appendix 4.

NEW BLEPHAROCERID MATERIAL

The material upon which the following tentative description is based, was made available too late to be included in Chapter I. As explained later, the material is such that the erection of a new genus is probably warranted.

Adult.

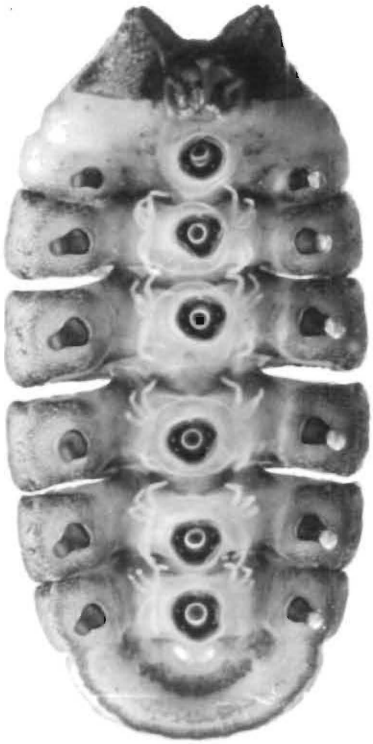
Male. (dissected from pupae - two specimens).

Head. Depth width ratio 1:1.4; eyes holoptic, eye ratio 1:1.5, upper facets larger than lower facets, upper and lower eye margins contiguous; ocellar turret not prominent; antennae 14-segmented, two proximal segments longer than wide, remainder wider than long; clypeus tapering distally; labrum very short; maxillary palpi apparently one-segmented, tubular, bearing 3-4 black hairs distally; galea very small; proximal segment of labial palp longer than labrum, distal segment shorter than proximal segment, overall length of labial palp 0.5 times head width; no lateral facial hairs.

Thorax. Mesothoracic segment prominent, colourless and bearing row of 15-25 hairs.

Wing. Approximately 6.0 mm. long, membraneous, densely covered with microtrichia, anal angle pronounced, forked Rs vein, veins Cu_1 and 1A not reaching margin.

Genitalia. Posterior lateral margin of cercus rounded, median concavity deep with convex sides; dististyles flattened ventrobasally, rising dorsally, thickest at midlength.



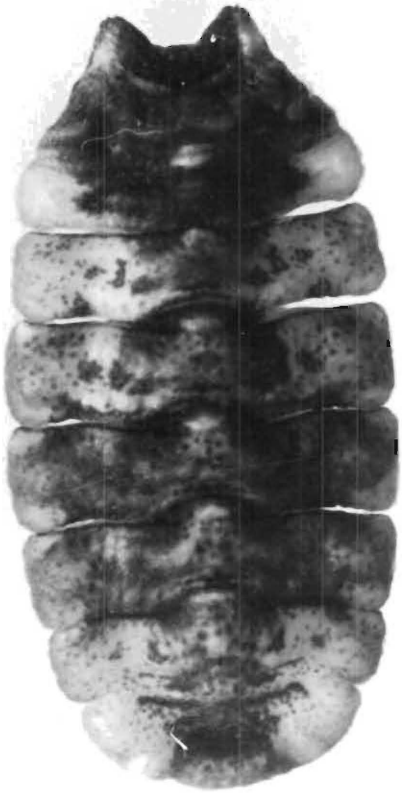


Plate 1.

Dorsal and ventral view of fourth instar larva of new blepharocerid.

Female. (dissected from pupae - two specimens).

Head. Depth width ratio 1:1.5, eyes dichoptic, eye ratio 1:2.7, upper facets smaller than lower facets; vertex area 0.32 times as wide as head width; ocellar turret constricted basally; antennae ?14-segmented; clypeus short; labrum extremely short; maxillary palpi apparently one-segmented, tubular, bearing 4-5 hairs distally; proximal labial palpi segment longer than labrum, distal segment small and converging; no lateral facial hairs.

Pupa.

Length 4.0-5.0 mm. Width 2.5-2.8 mm.
Flattened dorso-ventrally; dorsal portion of wing sheaths not embossed; pupal gills directed dorsally, almost contiguous medially; outer lamellae short, tapering sharply, inner lamellae smaller, often notched subapically; basal width length ratio of outer lamellae 1:2.

Larvae.

Fourth instar (Plate 1). Length 3.0-5.0 mm. Sucker width 0.36-0.45 mm.
Body divisions compressed antero-posteriorly, flattened dorso-ventrally, higher medially and laterally; cephalic division produced anterolaterally; cephalic sclerites dark reddish brown; colour pattern of remainder of body as in Plate 1, colour similar to N. tonnoiri; cephalic sclerites occupying 1/3 of cephalic division ventrally, only median portion dorsally; antennae situated on apex of cephalic division projections, inset and apparently one segmented; dorsal armature of small clear pustules irregularly arranged; cuticle of body extremely hard; no marginal armature; abdominal prolegs not extending beyond lateral margins, inset into cuticle, slightly longer than basal width, conical, bearing two hairs dorsally, possessing

internally small dorsal apodeme; 7th abdominal proleg reduced to two small hairs; posterior margin of anal division heavily sclerotised, sharply defined, not bearing hairs; 10 single tracheal gill filaments per body division, curved at midlength; anal gills small.

Third instar. Length 2.0-2.7 mm. Sucker width 0.20-0.25 mm. Six single tracheal gills per body division; body shape and other characters similar to fourth instar larva.

Second instar. Length 1.9 mm. Sucker width 0.15 mm. Body very flattened; median divisions sloping laterally, margins sharply defined and crenulate; anterior projections of cephalic divisions not pronounced; two long curved tracheal gill filaments per body division; otherwise very similar to the third and fourth instar larvae.

Locality Record.
Fuchsia Creek, Lower Buller Gorge, Westport. S31 167628, approx. 800 ft., L.P. I.D. McLellan, 18-vi-65, 23-xii-65, 11-vi-66, 2-vii-66, Cant. Mus.

The pharate adults of this new blepharocerid are very similar to the adults of Neocurupira campbelli, not only in size, but in the wing venation, trichation, and shape, head dimensions, shape of the antennal segments, and in the structure of the labial palpi and labrum. However, the shape of the maxillary palpi and the labrum, of the holoptic eyed males of the new blepharocerid are more similar to Horaia montana Tonnoir (1930) than to N. campbelli.

The pupa is of the type found in the Apistomyia, Elporia and Blepharocera (personal material) and is quite distinct from those of either Neocurupira or Horaia which are themselves very similar.

The larval instars, apart from the remarkable cephalic division projections and the position of the abdominal prolegs, are very similar, particularly in the second instar larva, to the larvae of Horaia spp. The general hardening of the body cuticle, the insertions of the abdominal prolegs and their internal apodemes, the peculiar tracheal gills and the heavily sclerotised distinct margin of the anal division are similar in both types. These characteristics are completely different from those of any other blepharocerid larvae, whereas the pupal and adult characteristics (apart from the maxillary palpi and labrum) are found in other subfamilies within the Blepharoceridae.

In this case it is believed that the similarities between the larvae of the new blepharocerid and Horaia indicate a phylogenetic relationship and that the similarities of the adult of the new form to Neocurupira campbelli are due to parallel evolution.

If this is the case then the presence in New Zealand of a blepharocerid closely related to Horaia supports the suggestion in Chapter I that New Zealand blepharocerids came from the north. However, it also means that there may have been two stocks of ancestral blepharocerids which invaded New Zealand during the Cretaceous; one of which gave rise to Neocurupira and Peritheates and the other to the Horaia - like blepharocerid.

The similarities of the adult to Neocurupira, the pupa to Apistomyia and other genera, and the larva to Horaia strengthens the case for a new genus, but it is suggested that an intensive search for further New Zealand blepharocerid forms be undertaken before any definite conclusions be made.

Tonnoir, A.L., 1930: Notes on Indian Blepharocerid Larvae and Pupae with remarks on the Morphology of Blepharocerid Larvae and Pupae in General. Rec.Indian Mus., 32, 2: 161-214.

APPENDIX 5.

Data for testing sampling technique at Purau.

Sample 1.

Length 4th Instar larvae.			Length pupae
9.9	7.5	9.1	5.6
9.2	8.8	8.3	6.1
8.3	9.4	8.8	6.8
9.3	5.4		6.5
9.9	8.3		6.3
9.6	8.4		6.9
8.8	10.5		7.2
8.8	5.4		6.6
8.8	4.3		6.8
9.1	6.9		
8.5	5.4		
9.7	5.9		
8.7	10.1		
9,6	8.1		
9.2	4.5		
9.0	9.1		
7.3	9.4		
8.3	4.5		
39			9 Total No.

Sample 2.

Length 4th Instar larvae.				Length pupae
7.9	9.1	5.9	7.1	6.1
9.6	7.1	7.2		6.1
7.6	8.4	7.6		6.3
8.3	9.6	9.0		6.6
9.0	9.6	9.6		6.3
6.5	7.9	7.6		5.9
5.9	9.2	6.5		5.7
6.3	8.3	8.4		6.2
7.0	7.6	9.0		6.6
6.9	7.8	6.5		5.6
9.1	5.9	9.2		6.2
7.2	8.5	5.3		6.3
8.5	7.3	4.1		6.2
5.7	7.5	4.7		6.3
7.4	6.8	8.4		6.8
8.5	7.2	8.1		
7.4	6.2	7.3		
7.6	7.6	9.2		
7.8	5.4	6.5		
7.3	6.8	5.0		
10.5	6.2	6.4		
64				15 Total No.

N. chiltoni

Kaituna.	♂	♀	Total
27.ix.64	12	12	24
18.xi.64	13	8	21
9.xii.64	11	5	16
3.i.65	26	13	39
4.ii.65	20	23	43
24.ii.65	6	10	16
21.iii.65	10	6	16
8.iv.65	10	10	20
27.iv.65	12	11	23
26.v.65	20	14	34
17.vi.65	7	5	12
6.vii.65	23	18	41
5.viii.65	12	14	26
9.ix.65	8	11	19
10.x.65	23	11	34
4.xi.65	19	6	25
24.xii.65	12	9	21
10.i.66	13	7	20
30.iii.66	6	12	18

APPENDIX 6.

Sex Ratio Data from Pharate Adult Collections.
(Only collections which contained 10 or more pharate adults have been used.)

N. chiltoni

Purau	♂	♀	Total
24.xi.65	9	2	11
4.xi.65	10	10	20
10.x.65	30	11	41
9.ix.65	22	16	38
5.viii.65	7	4	11
6.viii.65	9	13	22
24.ii.65	10	10	20
4.ii.65	23	8	31
6.i.65	19	19	38
14.xii.64	24	15	39
26.xi.64	11	14	25
3.xi.64	7	5	12
12.xii.63	16	10	26
30.xi.63	18	14	32
15.xi.63	7	12	19
27.x.63	14	8	22
8.x.63	10	8	18
22.ix.63	7	4	11
7.ix.63	8	4	12
15.viii.63	9	8	17
20.xi.62	9	1	10

N. campbelli

Bealey Chasm	♂	♀	Total
9.iii.65	56	33	89
19.i.65	8	12	20
21.xii.64	11	8	19
12.xi.64	21	8	29
16.vi.64	23	19	42
16.iv.64	10	14	24
22.iii.64	4	6	10
22.ii.64	67	33	100
1.ii.64	27	7	34
28.vi.63	7	7	14
25.v.63	6	9	15
28.iv.63	26	15	41
24.iii.63	52	18	70
19.i.63	54	15	69
15.xii.62	65	30	95

P. turrifer.

Bealey Chasm.			
19.i.65	8	3	11
22.ii.64	9	6	15
1.ii.64	14	11	25
14.xii.63	22	24	46
20.xi.63	13	11	24